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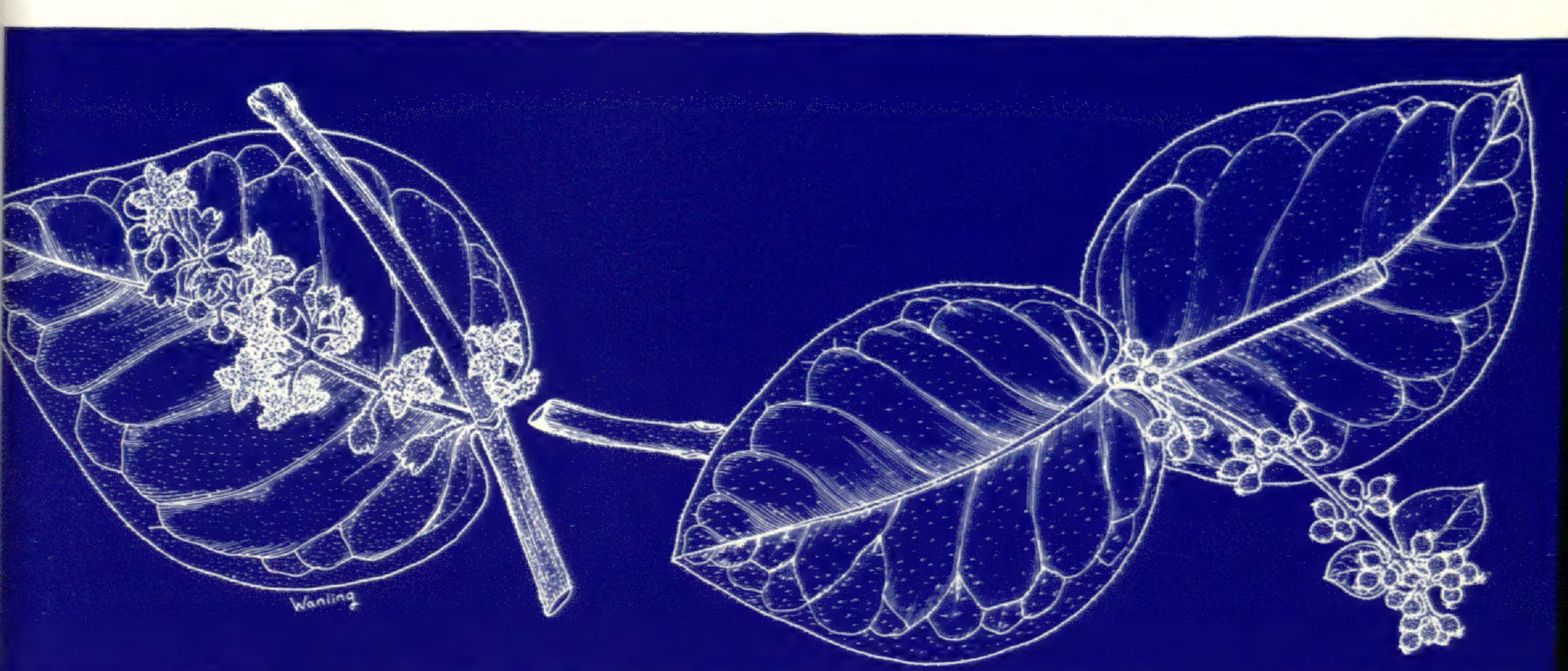

Monimia amplexicaulis Lorence

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A MONOGRAPH OF THE MONIMIACEAE (LAURALES) IN THE MALAGASY REGION (SOUTHWEST INDIAN OCEAN)[1,2,3]

DAVID H. LORENCE[4]

ABSTRACT

A systematic, ecological, and evolutionary study of the Monimiaceae of the islands in the Malagasy floristic region, southwest Indian Ocean (Madagascar and the Mascarene and Comore archipelagos), is presented. The Malagasy Monimiaceae are here taken to comprise four genera and 55 species, all endemic: *Monimia* (3 spp., Mascarenes); *Decarydendron* (3 spp., Madagascar); *Ephippiandra* (6 spp., Madagascar); *Tambourissa* (43 spp., Madagascar, Mascarenes, Comores). Madagascar, a large, ancient continental island, is the regional center of diversity with three genera and 35 species. The smaller, younger volcanic islands harbor fewer taxa: Mauritius (2/11); Réunion (2/5); Anjouan (1/2); Grand Comore (1/1); Mayotte (1/1); Mohéli (1/1); Rodrigues (0). Synopses of the family's taxonomic history, biogeography, and distribution are given. The regional setting is defined and summaries of the geology, geomorphology, and climate of each island given. Distribution of species according to habitat is discussed for each island and ecological observations are presented. Vegetative and floral morphology and anatomy are described from both the literature and original observations. A synopsis of the palynology is given. Cytological investigations of ten species of *Tambourissa* revealed all to have $n = 19$. Results were inconclusive for *Monimia* but suggest it is polyploid with $n =$ ca. 44–48. Field studies on floral biology of *Tambourissa* revealed that variations in floral morphology, color, and odor are responsible for several different pollination syndromes involving Coleoptera and Diptera. Breeding experiments demonstrated a strong tendency towards outcrossing via self-incompatibility in most monoecious species. Population density was related to pollinator systems in the three species studied.

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[1] Based on a Ph.D. dissertation submitted to the Graduate School of Arts and Sciences of Washington University, St. Louis, Missouri.

[2] I sincerely thank Alwyn H. Gentry for his continued support, advice, and criticism during the preparation of this monograph. I also thank Peter H. Raven, P. Goldblatt, W. D'Arcy, R. Sussman, B. Schaal, J. Dwyer, O. J. Sexton, P. J. Watson, M. Crosby, P. K. Endress, W. R. Philipson, and N. Morin for carefully reviewing and editing various stages of the manuscript or assisting me in various ways. I would like to thank the following individuals whose collaboration facilitated this study: R. E. Vaughan, J. Williams, R. Julien, J. Guého, and G. Lecordier, Mauritius Sugar Industry Research Institute, Mauritius; W. Owadally, T. A. M. Gardner, and M. D'Argent, Forestry Dept., Mauritius; J. Monty, Ministry of Agriculture, Mauritius; T. Cadet, Centre Universitaire, La Réunion; A. Rakotozafy, Parque Botanique, Tsimbazaza, Madagascar; P. Roulleau, Dept. of Agriculture, Mayotte; M. J. E. Coode, Royal Botanic Gardens, Kew; J. Bosser, Museum National d'Histoire Naturelle, Paris; P. K. Endress, Botanischer Garten und Institut für Systematische Botanik der Universität Zürich; P. Vinay and V. Zenger, Washington University; N. C. Pant, Commonwealth Institute of Entomology, London; Mrs. Wanling Peng for her excellent illustrations. I also thank the curators of the following herbaria for providing specimens: BM, G, K, MAD, MAU, MO, P, REU, TL-R, Z. Finally, I am particularly grateful to my wife, Ginette, for her assistance, companionship, and enduring support during this study.

[3] This work was supported by an NSF Doctoral Dissertation Improvement Grant (DEB 78-19954), a Sigma Xi Grant-in-Aid of Research, and a Washington University Graduate Fellowship, which are all gratefully acknowledged.

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In the taxonomic treatment, keys to genera and species are provided. Synonymy, descriptions, distribution, habitat, discussions, vernacular names, economic uses, and herbarium specimens are given for each species. *Hedycaryopsis* Dang. is united with *Ephippiandra* Decne., thus necessitating the following new name and combinations: *E. domatiata* Lorence (basionym: *H. capuronii* Cav.); *E. madagascariensis* (Cav.) Lorence; *E. perrieri* (Cav.) Lorence. *Ephippiandra capuronii* Cav. is transferred to *Tambourissa* as *T. beanjadensis* Lorence. Finally, *Phanerogonocarpus* Cav. is united with *Tambourissa* Sonn. and the following new names are proposed: *T. alaticarpa* Lorence (basionym: *P. perrieri* Cav.); *T. longicarpa* Lorence (basionym: *P. capuronii* Cav.).

This monograph represents a systematic, ecological, and evolutionary study of the Old World Monimiaceae (Laurales) occurring in the Malagasy floristic region of the southwestern Indian Ocean, here taken to include the microcontinental island of Madagascar and its satellite islands, the Mascarene and Comore archipelagos (Figs. 1, 2). On many of these islands Monimiaceae constitute an important woody element of the wet and cloud forest formations.

Monimiaceae were chosen for study because they are a large and diverse but poorly known family belonging to the so-called "woody Ranales" that have played a key role in interpretation of the morphological and evolutionary patterns of primitive angiosperms. Extensive adaptive radiation into four genera and some 55 species, all endemic, in the islands of this region suggests that the Monimiaceae hold a unique position as a model for island evolution by a relict group of plants. Study of the family is all the more imperative in view of the threat posed by man's destructive activities in the region coupled with the relentless invasive competition from introduced plant species.

In spite of their importance as floristic components on many of these islands, the Monimiaceae have never been the subject of a detailed field study. Not only has there been a dearth of knowledge regarding their ecology and biology, but lack of field studies has also resulted in considerable taxonomic confusion because of the difficulty in matching androecious and gynoecious flowering material and of understanding morphologically variable species.

During the course of this work I was able to spend an entire year in the Malagasy region studying and collecting Monimiaceae in their native habitats in the following islands: Mauritius (where the majority of the work was carried out), Réunion, Madagascar, Mayotte, and Grande Comore. As a result, I have seen about half the species in the field and have accumulated a great deal of new ecological and biological information that is incorporated into this monograph.

TAXONOMIC HISTORY OF THE MONIMIACEAE

The Monimiaceae sensu lato are an old and diverse assemblage of about 30 genera and nearly 350 species widely distributed in the tropics and subtropics, especially in the southern hemisphere. The family has undergone a great deal of taxonomic flux because of the striking diversity of its members, which display various combinations of primitive and advanced characters.

Evolutionary advancement in floral morphology of the Monimiaceae is generally expressed in terms of reduction, both in size and number of parts; in rearrangement of their orientation from spiral to radial and finally to decussate; in closure of the female floral receptacle; and also in a transition from free stalked carpels to an inferior syncarpous gynoecium (Corner, 1976). Other advanced trends occur in wood anatomy, with simplification of the vessel members; in pollen; in leaf architecture; and in a progression from floral bisexuality to monoecy and finally dioecy. The Monimiaceae have a long and interesting taxonomic history dating back nearly two centuries.

De Jussieu first founded the family in 1809 (as Monimieae) based on three previously described genera: *Monimia* Thouars, *Atherosperma* Labill., and *Siparuna* Aubl. (as *Citrosma* Ruiz & Pav.). Tulasne subsequently monographed the family in 1855 (1855b), including seven additional genera and subdividing it into three tribes on the basis of characters of the fruiting receptacle. Baillon (1868–1870) circumscribed the family in a much broader sense to include the present day Calycanthaceae and Gomortegaceae, defining five series or tribes: Calycantheae, Hortonieae, Tambourisseae, Atherospermeae, and Gomortegeae. Bentham and Hooker (1883) recognized only two tribes (Monimieae and Atherospermeae) based on features of the anthers and ovules, adding more genera but excluding the Calycanthaceae. This system was also followed by Pax (1891), who raised both tribes to the subfamilial level (Monimioideae and Ath-

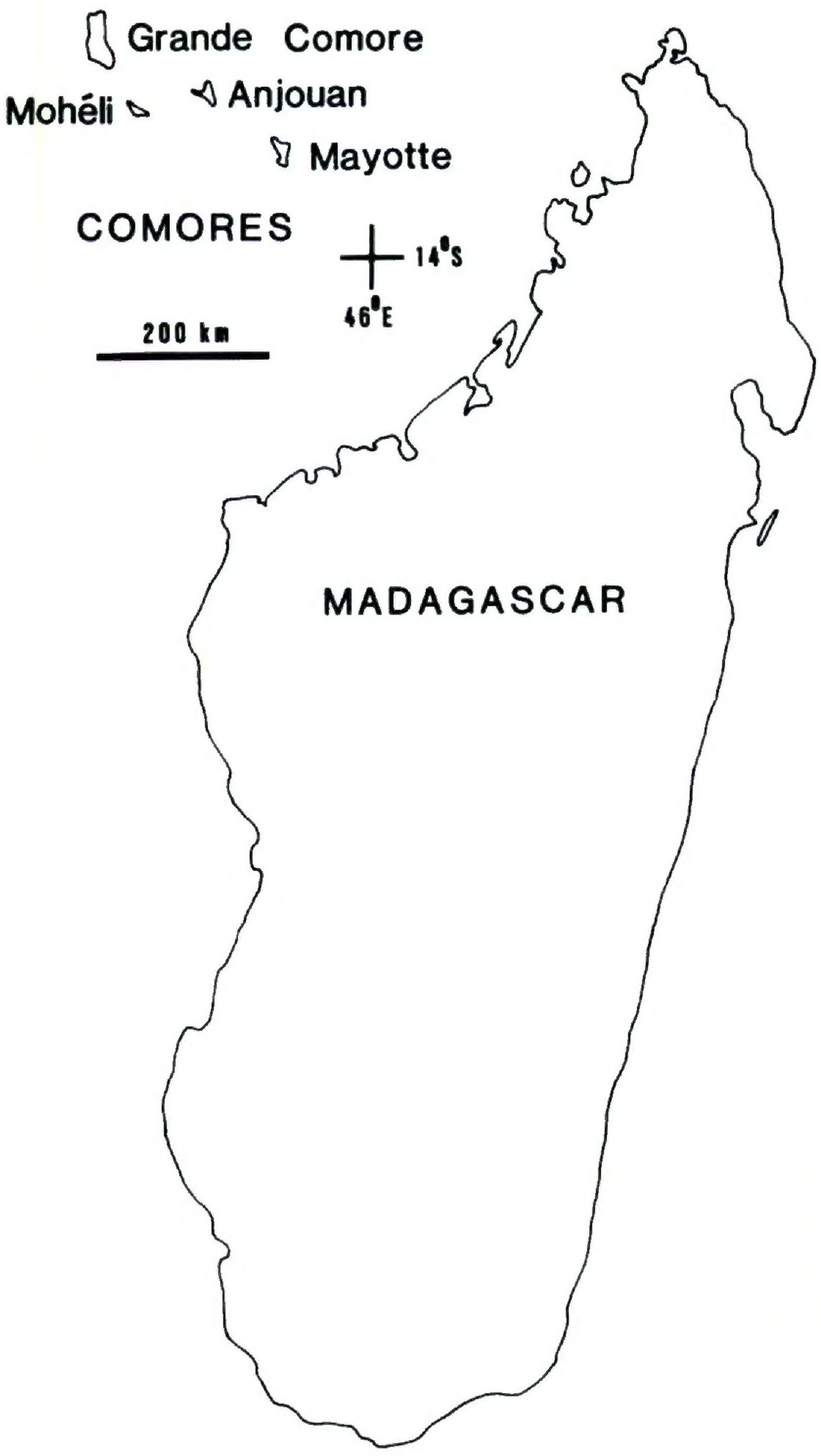


FIGURE 1. Regional map of study area, showing Madagascar and the Comore archipelago.

FIGURE 2. Regional map of study area, showing the Mascarene archipelago.

erospermoideae) and created six tribes for the species groups of Bentham and Hooker.

In their monograph of the family for "Das Pflanzenreich," Perkins and Gilg (1901) followed Pax, and Bentham and Hooker in recognizing two subfamilies but modified the tribes, creating an additional one under Monimioideae and merging two under Atherospermoideae. Perkins (1911) later updated the earlier revision using the same system. Hutchinson (1964) more or less followed Bentham and Hooker in dividing the Monimiaceae into two subfamilies, but recognized only four tribes.

As a result of its extreme diversity, many attempts have been made to dissolve the Monimiaceae sensu lato (Brown, 1814; Lindley, 1853; Pichon, 1948; Schodde, 1970; Smith, 1969). The truly extraneous elements, however, notably *Amborella, Austrobaileya,* and Trimeniaceae, have been removed from the family by workers such as Pichon (1948) and particularly Money et al. (1950) in their important study of the morphology and relationships of the family. I agree with Thorne (1974) that the Monimiaceae sensu lato comprise a rather large and variable but coherent group with at least five major evolutionary lines derived from now extinct common ancestors. Recent morphological and anatomical studies by Sampson (1969a, 1969b), Endress (1980a, 1980b), as well as those by Money et al. (1950), support the rationality of treating these lines as subfamilies belonging to a single, diverse family rather than pursuing the alternative of splitting them into five separate families.

Hortonioideae, the smallest subfamily, contains three species in the unique genus *Hortonia* endemic to Sri Lanka (Ceylon). Its members possess an elaborate perianth with spirally arranged petaloid and sepaloid series, floral bisexuality, free stalked carpels borne on a discoid receptacle, basal staminal appendages, helical banded pollen, primitive wood anatomy, and the gametic chromosome number $n = 19$ (Money et al., 1950; Goldblatt, 1974; Endress, 1980a). Because it has retained the greatest assemblage of primitive characters, it has been considered to be most representative of the ancestral condition (Money et al., 1950), although recent studies by Endress (1980a) suggest it occupies a position intermediate between the Atherospermoideae and the Monimiaceae sensu stricto (i.e., Mollinedioideae plus Monimioideae of Thorne).

Members of the next subfamily, Atherospermoideae, are linked to the Hortonioideae by the similarly petaloid perianth and floral bisexuality of some members, and by their separate carpels borne on a shallowly concave receptacle. Advancements over the Hortonioideae include whorled arrangement of the parts and reduction

in their number, and a tendency towards floral unisexuality. The Atherospermoideae are characterized by having bisporangiate valvate stamens, erect, basal ovules (usually), a single nodal trace, advanced wood anatomy, and a basic chromosome number of $x = 22$. These plants also possess 1–2-colpate pollen and show a trend towards specialized comose, wind-dispersed carpels. The five genera and 12 species of Atherospermoideae have a strongly disjunct austral distribution ranging from Australasia to Chile, emphasizing the subfamily's great antiquity.

The Siparunoideae are also characterized by bisporangiate valvate stamens, erect basal ovules, a single nodal trace and a basic chromosome number of $x = 22$. These features are similar to those found in the Atherospermoideae, and the two groups probably represent lines of parallel evolution from a common ancestral stock (e.g., Schodde, 1970). The Siparunoideae, however, lack the basal staminal appendages, septate wood fibers, and hippocrepiform sclerids of the Atherospermoideae. Furthermore, advanced trends such as vessels with simple perforation plates, and closed, reduced floral receptacles with a velum replacing the perianth occur in the Siparunoideae in addition to other differences such as inaperturate, granulate pollen and bird-dispersed carpels. The subfamily comprises three genera: *Siparuna* with about 160 species in tropical America, *Glossocalyx* with three species in west tropical Africa, and *Bracteanthus* with a single species in Brazil. Thorne (1974) suggested that *Bracteanthus* may merit tribal or subfamilial status, and that Glossocalyxoideae be recognized as a subfamily (Thorne, 1983).

The largest subfamily, Mollinedioideae, contains about 18 genera and over 145 species (Thorne, 1983). Its members are characterized by having apetalous, unisexual flowers displaying various degrees of reduction and specialization, relatively primitive wood anatomy, and gametic chromosome numbers of $n = 18$, 19, 22, ca. 38, ca. 43, and 57 for various genera (Goldblatt, 1974).

Thorne (1974) united *Monimia* (3 species, Mascarene Islands) with *Peumus* (monotypic, Chile) as the sole members of the subfamily Monimioideae. Both genera have paired basal appendages on the stamens; large, spinose pollen, and comparatively advanced wood anatomy. This seems to be the most rational placement of these two genera in light of the available evidence.

Although recent subfamilial revisions of the Monimiaceae have been adequate (e.g., Thorne, 1974), all have neglected treatment at the tribal level. As Perkins' (1911, 1925), Perkins and Gilg's (1901), and Hutchinson's (1964) treatments of the subfamilies and tribes are outdated, a critical reassessment of the subfamilies of Monimiaceae at the tribal level is urgently needed.

GEOLOGICAL HISTORY AND REGIONAL SETTING

Beginning with a Jurassic Gondwana supercontinent, the formation of the Indian Ocean commenced as Africa (with India and Madagascar) rotated away from South America at the start of the Cretaceous (summarized by Fisher et al., 1967). At the same time the Antarctica-Australia mass began drifting southward, whereas the block comprising Africa-India-Madagascar remained intact until the mid-Cretaceous prior to about 90 Ma (Raven, 1979). At that time Madagascar occupied a position against the present Kenya-Somalia coast and was part of a Malagasy-Mascarene subcontinent joined to India via the now largely submerged Mascarene Plateau (Axelrod & Raven, 1978). Separation of this subcontinent from Africa occurred during the mid- to late Cretaceous at about 90 Ma (Raven, 1979). Probable separation of India from the Malagasy-Mascarene subcontinent occurred at the onset of its northward movement, about 70 Ma, which continued until it collided with the Asian landmass at about 45 Ma (Raven, 1979).

Formation of the present crescent-shaped Mascarene Plateau began with the separation of a portion of continental crust from Madagascar in the late Cretaceous or early Tertiary as Madagascar moved southward (Fisher et al., 1967; Kutina, 1975; Wild, 1975). This fragment, composed of Precambrian granites, included the present Seychelles archipelago and possibly the entire western flank of the Mascarene Plateau above the Saya de Malha bank (Fisher et al., 1967). Formation of the remaining portion of the Mascarene Plateau from the Saya de Malha southward to Mauritius was probably accomplished by late Cretaceous-early Tertiary submarine volcanic extrusions (Fisher et al., 1967).

The Rodrigues Ridge, from which Rodrigues Island emerges, is parallel to a fracture zone extending eastward across the Midoceanic ridge complex and was probably formed during the late Tertiary (Fisher et al., 1967). It is a volcanic

entity distinct from the Mascarene Plateau, separating the latter from Mauritius and Réunion (Fig. 2).

The Comore archipelago, situated between Madagascar and Africa (Fig. 1), is a product of successive Pliocene-Pleistocene volcanic eruptions (Esson et al., 1970). In contrast to Madagascar, which is a continental island, the Mascarenes and Comores are volcanic in origin and therefore strictly oceanic in nature.

Geomorphology and Climate

At present Madagascar is separated from the African mainland by the Mozambique channel, some 500 km wide at its narrowest point (Fig. 1). Situated midway between Africa and the northern part of Madagascar and separated on either side by depths of ca. 3,000 m are the four islands comprising the Comore archipelago: Mayotte, Anjouan, Mohéli, and Grande Comore. Stretching from ca. 800 to 1,600 km due east of Madagascar lies the Mascarene archipelago comprising the islands of Réunion, Mauritius, and Rodrigues. The Mascarenes are separated from the nearest landmass, Madagascar, by a stretch of ocean ca. 4,000–5,000 m deep.

MADAGASCAR

As the world's third largest island with an area of 590,000 km², Madagascar is truly continental in nature, consisting of a fragment of the original Gondwana landmass. Its large size, insular nature, and long isolation have made it an important refugium for many unique and relictual groups of plants and animals, including the lemurs. Its former connection to Africa and India once provided a route for Cretaceous dinosaurs and the rich angiosperm floras that appeared at that time (Raven & Axelrod, 1978).

Geologically, Madagascar is composed of four elements (Brenon, 1972). A much folded and outcropping metamorphic Precambrian basement in the form of a peneplain comprises the rugged central plateau which rises above 1,000 m (range 800–1,500 m) and also the highest mountains which are under 3,000 m (2,876 m at the Tsaratanana massif). This basement drops off abruptly along the great eastern escarpment down to a narrow coastal plain. Secondly, a slightly tilted Permo-Carboniferous continental sedimentary formation belonging to the Karroo system overlies the Precambrian basement and forms a band along the western third of the island. Thirdly, basaltic volcanic formations belonging to upper Cretaceous eruptions form extensive flows in parts of the eastern and western regions and have given rise to certain mountain complexes in the north, center, and south of Madagascar. Finally, weathering and laterization of the Precambrian basement has resulted in a mantle of lateritic clays averaging 10–15 m thick overlying the bedrock. This is undergoing massive erosion accelerated by historic removal of much of the island's vegetation by man.

Madagascar's diverse geomorphology is the result of submersion and uplifting, pedogenesis and erosion, and scattered vulcanism during its long history. This edaphic diversity coupled with a variety of climatic types has resulted in the wide spectrum of habitats that exists in Madagascar.

Madagascar's position, considerable size (590,000 km²), and close juxtaposition of physical features such as lowland coastal plains gradually or steeply sloping to areas of medium altitude, and mountains exceeding 2,500 m elevation, are all responsible for its considerable climatic diversity (Donque, 1972).

First, its insular nature provides a maritime environment which is most prevalent in the eastern region. Here, warm oceanic currents moderate the temperature while moisture-laden trade winds and tropical cyclones impinging upon the east coast deposit heavy rains along the coast and eastern escarpment, permitting the development of dense, evergreen wet forest which forms a zone along the eastern third of Madagascar.

Second, Madagascar is sufficiently long (ca. 1,500 km) and wide (ca. 450 km average) to display many characteristics of a small continent. This continentality is reflected in a wide spectrum of temperature, atmospheric humidity, precipitation, and wind regimes. As a result of its longitudinal extension, the island possesses subequatorial regions in the north (at 12°S) where a monsoon climate and dry season modify the composition of the evergreen forest. In the south, it passes through the Tropic of Capricorn and extends into the subtropics at its southern extremity (25°30′S), giving rise to considerable thermal variation. On a latitudinal basis, both precipitation and temperature decrease considerably in the central uplands. Precipitation further decreases and temperature increases to the west and south as the Trade winds rapidly lose their remaining moisture and velocity due to the rain shadow effect. As a result, the vegetation

TABLE 1. Distribution of total Monimiaceae and *Tambourissa* species per island in the Malagasy region in relation to area, elevation, and age of island.

Island	Area (km^2)	Elevation (m)	Age (Ma)	Total Species Monimiaceae	Total Species *Tambourissa*
Madagascar	590,000	3,000	70† (as island)	35	26
Réunion	2,500	3,000	3.0	5	2
Mauritius	1,865	900	7.8	11	10
Grande Comore	1,148	2,400	0.01†	1	1
Anjouan	424	1,600	1.5	2	2
Mayotte	370	700	3.7	1	1
Mohéli	290	800	ca. 1.5	1	1
Rodrigues	110	400	1.5	0	0

becomes progressively more xeric in nature to the south and west, passing from sclerophyllous evergreen forest to semideciduous forest and finally thorn scrub and desert (Koechelin et al., 1974, give a detailed account of the vegetation).

Temperature, wind, and rainfall are further influenced by the island's varied relief, giving rise to a spectrum of bioclimates varying in both temperature and precipitation. For example, some of the higher mountains extend into the cloud zone and harbor a montane cloud forest formation, above which occurs a low, ericoid scrub characteristic of the high montane zone.

This diversity of habitats and extreme ecological gradients in conjunction with Madagascar's long isolation have resulted in high levels of floristic endemism: up to 48% of the genera and 95% of the species are endemic in certain regions (Koechelin et al., 1974; Leroy, 1978). It is therefore not surprising that Madagascar harbors the greatest constellation of Monimiaceous taxa in the region (three genera and ca. 35 species), Africa notwithstanding (Table 1).

MASCARENE ARCHIPELAGO

The three Mascarenes are volcanic oceanic islands that consist of the exposed summits of submarine mountain chains, i.e., Mauritius and Rodrigues, and an isolated volcano arising from an abyssal submarine plain, i.e., Réunion (Cadet, 1977).

All three islands experience a tropical insular climate moderated by the maritime effects of the warm ocean and the steady south-east Trade wind regime. Precipitation is most abundant during the warm and rainy austral summer season lasting from December to April, occurring as orographic rains resulting from adiabatic air expansion, and also as heavy cyclonic rains. In addition to bringing rain, cyclones, with winds gusting up to 240–320 km/hr, are often destructive to the vegetation. On the average, direct hits by cyclones occur only once every 12 to 15 years. The relatively drier and cooler austral winter season lasts from May to November.

The mean annual precipitation ranges from 1,100 to 1,700 mm in Rodrigues (Lorence, 1976), and from 1,000 to 5,000 mm in Mauritius and Réunion (Lorence, 1978; Cadet, 1977). Mean annual temperatures in the Mascarenes are not extreme, ranging from 16 to 20°C in the uplands and from 21 to 25°C in the lowlands during the winter, and from 21 to 25°C in the uplands and 27 to 30°C in the lowlands during the summer.

Réunion, the largest (2,500 km^2) and easternmost of the Mascarene Islands, is the summit of a volcanic cone rising some 3,000 m above sea level. Its active volcano, Piton de la Fournaise, still erupts frequently, emitting basaltic lavas similar to the Pleistocene flows in Mauritius (Fisher et al., 1967). Quaternary lavas from the Piton des Neiges flows have been dated at 2.1 Ma, although Fisher et al. (1967) suggest that submerged caldera flows may be older, possibly ca. 3 Ma (Cadet, 1977). Some subsidence appears to have taken place during the Quaternary, perhaps resulting in a small reduction of the island's surface area. Coral reef development around Réunion is virtually absent.

In addition to its accentuated relief, Réunion's 3,000 m altitude provides the greatest range of habitats of any of the Mascarenes, ranging from semideciduous dry forest and thicket in the western rain shadow, to lowland wet forest, montane cloud forest and high montane ericoid scrub and grassland. *Tambourissa,* with only two species here, is less abundant and much less diverse than

in Mauritius (10 species; Table 1). It is significant, however, that *Monimia* reaches its greatest diversity and abundance here, with three species often forming locally abundant or dominant elements of the wet and cloud forest formations. Much of the upland vegetation in Réunion is still intact, but little remains in the lowlands.

Mauritius, the central island, is second largest with an area of 1,865 km² and a maximum altitude just under 900 m. By far the oldest of the three Mascarenes, its earliest lavas are Pliocene, dating to 7.8 Ma (McDougall & Chamalaun, 1969), and its vulcanism ended about 100,000 years ago during the Pleistocene. During its long history, erosion has moderated the island's relief which consists of a central plateau fringed by a discontinuous mountain range dipping down to coastal plains in all but the southern sector. Except for its well-developed fringing coral reefs, Mauritius is completely volcanic in origin and composed of alkali olivine basalts deposited in three main strata. The presence of coral deposits at altitudes of up to 100 m above sea level on the mainland suggests past fluctuations in the sea level, although progressive subsidence seems to be the case (Fisher et al., 1967). If the submarine plateau surrounding Mauritius is taken into consideration, the island's previous area was probably ca. 2,500 km² during the lowered sea levels of the Quaternary (comparable to Réunion's present area), as opposed to its 1,865 km² today. It seems that earlier in the island's history its relief was more accentuated than today but probably did not exceed 1,000 m in altitude during the last 3.5 Ma (Cadet, 1977).

Mauritius supports a fairly diverse array of plant communities, notably semideciduous dry forest in the western rain shadow area, lowland and lower montane evergreen wet forest, small areas of cloud forest on the highest mountains, and patches of heath formation (Lorence, 1978).

Next to Madagascar, Mauritius harbors the most species of *Tambourissa* (10). In contrast, *Monimia,* which is essentially a genus of cloud forests, is poorly represented with a single species in Mauritius, perhaps because of its low altitude. Representative areas of most of the island's plant communities are still preserved by way of nature reserves and crown land, but many of these have been irreversibly degraded by invasive exotic plant species.

Rodrigues is the smallest and westernmost of the Mascarenes, with an area of only 110 km² and an altitude just under 400 m. A ridge composed of a uniform series of alkali olivine basalt flows whose exposed parts do not exceed 1.54 Ma (McDougall et al., 1965), it has apparently undergone extensive subsidence since its formation and probably once occupied nearly ten times its present area (Cadet, 1977). Now only the summit of a large submarine platform remains exposed, supporting large, well-developed fringing coral reefs. In view of its high specific level of floristic endemism, equalling the other two Mascarenes, Rodrigues could be older than Réunion but younger than Mauritius (Cadet, 1977), contrary to the suggestion put forth by McDougall et al. (1965).

Because of its small size and low elevation, Rodrigues is ecologically the least diverse of the Mascarenes. Most of the island was once covered by a low evergreen moist or wet forest, drier on its leeward western side, although sections of uplifted coralline calcarenite support an interesting scrub formation. Although a species of *Monimia* was supposedly collected in Rodrigues, no substantiated records of Monimiaceae are known from the island. This is probably because of its isolation and paucity of the proper habitats. Also, nearly all of Rodrigues' indigenous vegetation has been destroyed by man.

COMORE ARCHIPELAGO

The Comores are a group of four volcanic islands located in the Mozambique channel midway between Madagascar and Mozambique on the east African coast. Situated on a submarine ridge, they are the product of successive volcanic eruptions extending from southeast to northwest and are no older than the Pliocene-Pleistocene (Guilcher et al., 1965; Hajash & Armstrong, 1972). Analogous to the Mascarenes, the Comores differ in being more closely spaced (separated by distances no greater than 65 km; Fig. 1), are closer to major landmasses, and are on the average smaller and younger (Esson et al., 1970).

Mayotte is the most southeasterly, the oldest (ca. 3.65 Ma), and most highly eroded of the four islands. With an area of 370 km² and a maximum altitude of 660 m, it consists of a succession of old lava flows from at least two volcanic eruptions (basaltic and phonolitic) which gave rise to the bulk of the island. Following periods of relative stability, a final period of vulcanism poured lava across the eastern part of the island. Other indications of Mayotte's relatively advanced age

within the archipelago are a highly embayed coastline, development of the finest barrier reef and lagoon in the Indian Ocean, and occurrence of deep, red laterized soils (Guilcher et al., 1965).

Anjouan and Mohéli are both centrally located and represent the summits of extinct volcanos. Both are relatively old structures with eroded but still recognizable craters and cones. Anjouan is larger, attaining 1,595 m, and has an area of 424 km^2 with an accentuated relief and narrow but fringing coral reefs emcompassing about two-thirds of the coastline. Its oldest lavas have been dated at 1.52 Ma (Hajash & Armstrong,1972). Mohéli is the smallest of the Comores, rising to 790 m altitude with an area of only 290 km^2. Its relief is less rugged but its reefs are also wide and well developed, although its lavas have not been dated. Mayotte, Anjouan, and Mohéli are all volcanically extinct.

Grande Comore, largest (1,148 km^2) and youngest of the four islands, has an active volcano whose summit attains 2,360 m, and is essentially a mass of scarcely eroded lava lacking permanent rivers and streams. The only dated lavas from Grande Comore are recent (0.01 Ma), although underlying flows are thought to be older (Hajash & Armstrong, 1972). Coral reef development around the island is sparse and embryonic, also reflecting its relative youth.

The Comores lie in the south-east Trade wind belt, although they are somewhat sheltered by Madagascar, and cyclones are rare. The drier and cooler winter season extends from May to October, the majority of the rain falling during the hot austral summer season from November to April (Manicacci, 1939). In 1935, the following annual rainfalls were recorded: Grande Comore, 4,254 mm; Anjouan, 1,411 mm; Mayotte, 869 mm (at Dzaoudzi, but probably double inland); Mohéli, 478 mm (Manicacci, 1939). Temperatures range from 25 to 35°C in the summer and from 18 to 25°C in the winter, depending on the elevation.

The Comores generally support evergreen moist or wet forest on their lower windward and mountainous slopes, and semideciduous dry forest in the low altitude regions of the rain shadow. Anjouan and Grande Comore have zones of cloud forest above 900 or 1,000 m, and this gives way to *Philippia* heath formation on the Karthala volcano massif on Grande Comore. Each island has but a single species of *Tambourissa,* except for Anjouan which has two (Table 1). Four of the five Comorean species of *Tambourissa* appear to be closely related and may be derived from a common ancestor.

Biogeography and Distribution

Biogeographically, it appears that direct migration of the Monimiaceae between Africa and South America occurred by the Eocene, after which widespread extinction took place in Africa (Raven & Axelrod, 1974; Axelrod & Raven, 1978). Fossils that have been considered Monimiaceous are known from the late Cretaceous (ca. 70–80 Ma) in Europe, Africa, and Argentina. In contrast to the widespread floral and faunal impoverishment that took place in continental tropical Africa (Richards, 1973, 1979), the Malagasy region provided an important refuge for many elements of the area's biota; for example, the lemurs in Madagascar and the Comores, and the now extinct flightless birds such as the dodo and solitaire in the Mascarenes (Carlquist, 1965).

The Monimiaceae may be thought of as botanical counterparts of the lemurs and are represented by four genera and about 55 species in the Malagasy region, all endemic. The isolation and habitat diversity offered by islands are well known to be conducive to rapid adaptive radiation (e.g., Carlquist, 1965, 1974), which is exemplified by the Malagasy area Monimiaceae. In marked contrast, only two genera of Monimiaceae have persisted in continental Africa—i.e., *Glossocalyx* and *Xymalos*—comprising a total of four species. This is primarily because the Monimiaceae attain their greatest diversity in premontane wet and montane cloud forest formations, habitats that are abundant in the Malagasy region but poorly represented in Africa. Furthermore, most cannot tolerate the ecologically significant dry periods that are characteristic of even the wet forest in Africa (Richards, 1973), although their absence from the cloud forests of the east African mountains is puzzling. Perhaps these forests were greatly reduced in extent during the dry periods of the Pleistocene, and Monimiaceae were unable to recolonize them from their more equable refuge areas on Madagascar and the Mascarenes.

Madagascar harbors three closely allied genera of trees and shrubs belonging to the subfamily Mollinedioideae. Of these, *Ephippiandra* (6 spp.) and *Decarydendron* (3 spp.), are endemic. Their inability to spread to the other islands may be a reflection of their poor dispersibility or seed viability. Alternatively, suitable habitats may be

lacking on the satellite islands. This does not appear to be the case, however, because relatively large and elevated islands such as Réunion and Mauritius offer many of the same habitats as Madagascar (Table 1).

Tambourissa, however, has reached six of the seven satellite islands where it has become established and undergone successful adaptive radiation (Table 1). Reports that *Tambourissa* occurs in Java (e.g., Cavaco, 1965) appear to be erroneous (see discussion under *T. ficus*), and the genus appears to be restricted to the Malagasy floristic region. Possible reasons for its success most likely include its bright red-orange drupes, which are ostensibly more attractive to birds (those of *Ephippiandra* ripen black) resulting in greater dispersibility, a greater seed viability (drupes of *Tambourissa* may take two or three months to germinate; D. Lorence, pers. observ.), and enhanced ability to compete and evolve rapidly. In any case, *Tambourissa* provides an excellent model for island evolution in a family of primitive angiosperms.

Monimia (Monimioideae) consists of three closely related species endemic to the Mascarene Islands of Mauritius and Réunion. Its absence from Madagascar is puzzling in view of its bird-dispersed carpels. *Peumus* in Chile appears to be its closest relative, although it also shares a number of features with *Palmeria* from Oceania (see discussion under *Monimia*).

Habitat and Ecology

The majority of ecological and floristic studies or surveys conducted for the islands of the Malagasy region demonstrate or at least mention the importance of the Monimiaceae as woody elements of the vegetation (Vaughan & Wiehe, 1937, 1941; Humbert, 1965; Legris, 1969; Koechlin, 1972; Koechlin et al., 1974; Cadet, 1977). In addition, data from specimens provide much information.

MADAGASCAR

Although I am unaware of any specific ecological studies for Madagascar involving Monimiaceae, the broad vegetational surveys of Humbert (1965) and Koechlin et al. (1974) coupled with data from specimens which I have examined and those cited by Cavaco (1959) have enabled the habitat and distribution of most species to be established. A significant number of taxa, however, are known from only one or several collections, possibly a result of undercollecting, which may therefore inaccurately portray their actual distributions. Of the Imperfectly Known *Tambourissa* species, only numbers 40 (*T.* sp. A) and 42 (*T.* sp. C), are included in this discussion, because collection localities for the others are either too vague or were not located.

Work done by Humbert (1965) and Koechlin et al. (1974) indicates that in Madagascar species of *Tambourissa,* along with *Weinmannia* (Cunoniaceae), are among the most frequent and characteristic components of the canopy in the montane wet/cloud forest zone. *Tambourissa* attains its greatest diversity here, with at least 14 of the island's 26 species occurring in this zone (Table 2) which forms a belt along the eastern part of the island from ca. 800 m and extends upward to the mountains of the central plateau to between 1,300 and 1,800 m. Annual precipitation here ranges from ca. 1,000 to 2,000 mm, with a short dry season.

In addition to *Tambourissa,* two endemic Madagascan genera also occur in this zone, *Decarydendron* (2 spp.) and *Ephippiandra* (3 spp.), bringing the total number of Monimiaceae to 19 (Table 2). The *Tambourissa/Weinmannia* zone is clearly Madagascar's richest habitat in terms of Monimiaceae species and genera.

In the east, this zone is subtended by a lowland wet forest of Myristicaceae and *Anthostema* (Euphorbiaceae) receiving an annual precipitation of ca. 1,500–3,500 mm and having no significant dry season. In addition to sharing about three species with the former zone, including *Ephippiandra madagascariensis* and two species of *Tambourissa,* this zone possesses a number of its own species, most notably *Decarydendron lamii* and five species of *Tambourissa*: *T. alaticarpa, T. castri-delphinii, T. decaryana, T. longicarpa,* and *T.* sp. C. Besides *T. castri-delphinii,* the wide-ranging *T. purpurea* and *T. religiosa* are the only Monimiaceae known to inhabit the coastal forests on sand dunes.

The lowland wet forest also extends to the small Sambirano region in the northwest, including Nosy Be Island, where it is further characterized by the presence of many Chlaenaceae, an endemic family. In addition to harboring such wide-ranging species as *Ephippiandra madagascariensis* and *Tambourissa purpurea,* the Sambirano area has two endemics: *T. nitida* and *T. nosybensis.*

At altitudes from ca. 1,800 to 2,000 m in the cloud zone on the mountains of the central re-

TABLE 2. Distribution of Monimiaceae according to habitat in Madagascar.

1. Lowland wet forest zone of Myristicaceae and *Anthostema* (ca. 0–800 m), including littoral forest and Sambirano region.
   Decarydendron lamii
   Ephippiandra madagascariensis
   Tambourissa alaticarpa
   T. castri-delphinii
   T. decaryana
   T. longicarpa
   T. nitida
   T. nosybensis
   T. perrieri
   T. purpurea
   T. religiosa
   T. sp. C (no. 42)
2. Medium altitude wet/cloud forest zone of *Tambourissa* and *Weinmannia* [ca. 800–1,300(–1,800) m].
   Decarydendron helenae
   D. perrieri
   Ephippiandra domatiata
   E. madagascariensis
   E. microphylla
   Tambourissa beanjadensis
   T. capuronii
   T. floricostata
   T. gracilis
   T. hildebrandtii
   T. humbertii
   T. madagascariensis
   T. perrieri
   T. purpurea
   T. religiosa
   T. thouvenotii
   T. trichophylla
   T. uapacifolia
   T. sp. A (no. 40)
3. Sclerophyllous montane lichen forest zone (central mountains, 1,300–2,000 m).
   Ephippiandra myrtoidea
   E. perrieri
   E. tsaratanensis
   Tambourissa gracilis
   T. parvifolia
4. High montane *Philippia* ericoid heath formation (central mountains, above ca. 2,000 m).
   Ephippiandra microphylla
   E. perrieri
   Tambourissa parvifolia
5. Sclerophyllous moist forest zone of *Uapaca bojeri* and Chlaenaceae (western slopes of central domain, up to ca. 800–900 m).
   Tambourissa hildebrandtii
   T. purpurea
6. Semideciduous dry forest zone of western domain (below ca. 700–800 m).
   Tambourissa bathiei (probably riverine)
   T. perrieri (probably riverine)

TABLE 2. Continued.

gion, the *Tambourissa/Weinmannia* belt is replaced by a dense sclerophyllous forest with an abundance of epiphytic lichens. Perhaps because of the lower temperatures, the Monimiaceae drop out rapidly here (Table 2). *Ephippiandra microphylla* and *Tambourissa gracilis* are virtually the only species shared with the zone below. The only species characteristic of this zone and, to a lesser extent, of the high montane ericoid thicket superseding it beyond the cloud zone at above ca. 2,000 m are *Ephippiandra myrtoidea, E. perrieri, E. tsaratanensis,* and *Tambourissa parvifolia.*

The western slopes of the central plateau at and below ca. 800–900 m are characterized by a hotter, drier climate with more extreme temperatures. This area supports sclerophyllous forest of *Uapaca bojeri* (Euphorbiaceae) and Chlaenaceae, with only *Tambourissa hildebrandtii* and *T. purpurea,* two of the most widespread species, able to persist here.

In the dry western regions that extend to the coast, the sclerophyllous forest is gradually replaced by a semideciduous dry forest of *Dalbergia, Commiphora,* and *Hildegardia.* The only Monimiaceae found here are *Tambourissa bathiei* and *T. perrieri,* which apparently occur in riverine forests.

It should be emphasized that the vegetation of Madagascar, like most of the other islands, has undergone and continues to undergo severe degradation and destruction under the influence of man (Rauh, 1979). Because of its size, however, remnants of most and even fairly extensive areas of some vegetation types still remain (Rakotozafy, pers. comm.), but the need for their conservation is essential.

MASCARENE ISLANDS

On the average larger and older than the Comores, the Mascarene Islands also harbor more genera (two) and species (15) of Monimiaceae despite their greater isolation. In addition, the Mascarenes have been comparatively well stud-

ied floristically (Baker, 1877; Balfour, 1879; Cordemoy, 1895; "Flore des Mascareignes," in progress) and ecologically (Vaughan & Wiehe, 1937, 1939, 1941; Wiehe, 1949; Rivals, 1952; Cadet, 1977), thus permitting a more definitive assessment of the family's status there.

RÉUNION

Réunion is analogous to Grande Comore in being the only volcanically active member of its archipelago but is larger and older, supporting two genera and five species of Monimiaceae in contrast to the latter's unique species. Cadet's (1977) comprehensive study of the island's vegetation emphasizes the importance of the family as woody components of the flora. Although harboring the greatest expanse of indigenous forest of the three Mascarenes, many areas of Réunion are undergoing a dramatic invasion by vigorous exotic species such as *Psidium, Rubus,* and *Furcraea,* similar to that occurring in the other two islands.

Much of Réunion's lowland forest has disappeared, particularly in the dry western sector. Fairly extensive areas of lowland wet forest ("forêt mégatherme hygrophile" sensu Cadet, 1977) still remain above ca. 300 m, however, on the southern slopes of the active volcano, Piton de la Fournaise (at Mare Longue, Brûlé de Baril and other areas). Here a lush wet forest dominated by Sapotaceae (*Labourdonnaisia, Mimusops,* and *Sideroxylon*) has become established on the mosaic of lava flows where the rainfall averages 4,000–5,000 mm per year. *Tambourissa elliptica* subsp. *micrantha* appears here at ca. 300 m as a local, occasional to common component of the middle and upper strata and ranges to the mid or rarely upper limits of the wet forest zone (ca. 800–1,000 m) where it is generally replaced by *T. elliptica* subsp. *elliptica.* The latter is characteristically a smaller understory tree or treelet of occasional to common occurrence in both the wet forest zone below 1,100 m and the cloud forest zones (ca. 1,100–2,000 m) (Fig. 31).

The only other species to occur in the lowland wet forest zone of Réunion is *Monimia ovalifolia,* which appears at ca. 500 m and extends to ca. 1,700 m in the cloud forest zone. It typically forms local populations on sheltered slopes and in valleys and may become a canopy tree.

The lower limits of the cloud belt lie at ca. 800–1,100 m and mark the transition from wet to cloud forest ("forêt mésotherme hygrophile" of Cadet), a zone characterized by lower temperatures and relatively constant high humidity. It is in the cloud forests of Réunion that *Monimia* attains its greatest abundance and diversity. The climax is considered to be the *Monimia/Dombeya* association ("Bois de couleurs") although *Acacia heterophylla* Willd. is dominant in some areas (Cadet, 1977).

Of the three *Monimia* species occurring in this zone, *M. rotundifolia* is by far the most abundant and widespread, codominant in many areas with species of *Dombeya* (Sterculiaceae) and other genera, e.g., at Col de Bellevue and Bébour forest (Fig. 22). Mature individuals 8–16 m high with dense, spreading crowns are often major components of the mid stratum and canopy. It occurs less frequently in the *Acacia/Nastus* forest and occasionally in *Philippia* heath up to ca. 2,000 m, with its lower limit extending down to ca. 1,000–1,100 m at the interface with lower altitude wet forest.

Monimia amplexicaulis is more restricted in distribution than *M. rotundifolia* and is generally confined to the mid and upper limits of the cloud forest, occasionally with *Acacia.* It characteristically forms discrete populations on the sheltered, leeward escarpments of the "cirques" or ancient volcanic calderas and is known primarily from the following localities where it usually replaces *M. rotundifolia*: Hauts du Tévelave, Plaine des Cafres, and Cirque de Cilaos (Fig. 22). An example of ecological differentiation between the two species was studied at Hauts du Tévelave, where *Monimia amplexicaulis* begins to replace *M. rotundifolia,* which occurs alone below ca. 1,700 m. Here, both species occur sympatrically at ca. 1,700 m along the Domanial line (Ligne Dominicale); neither intermediates nor hybrids were observed among dozens of individuals examined. The two species are easily recognized in the field and appear to maintain their integrity by flowering at different times.

Monimia ovalifolia is an occasional tree up to ca. 1,700 m altitude but is rarely abundant. It occurs sympatrically with *M. rotundifolia* in many localities, e.g., at Bébour forest where both species remain distinct and have different flowering times (Fig. 22).

Only two species of *Tambourissa* occur in the cloud zone: *T. crassa* and the macrophyllous upland form of *T. elliptica* subsp. *elliptica. Tambourissa crassa* is a light-demanding small tree which occupies the upper stratum of low forest or occurs in relatively open mixed heath at 1,200–

TABLE 3. Occurrence of Monimiaceae species according to habitat in Mauritius: indigenous plant communities.

	Philippia Heath:	*Sideroxylon* Wet Forest:		High Forest:		Cloud Forest:	Semideciduous Dry Forest:
	Pétrin; 660 m, pptn. 4,000 mm	Pieter Both; 550 m, pptn. 2,400 mm	Bel Ombre; 300 m, pptn. 2,400 mm	Macabé; 660 m, pptn. 3,200 mm	Brise Fer; 600 m, pptn. 2,400 mm	Mt. Cocotte; 760 m, pptn. 5,000 mm	Yemen; 200 m, pptn. 1,600 mm
Monimia ovalifolia						X	
Tambourissa amplifolia			X	X			
T. cocottensis						X	
T. cordifolia	X						
T. ficus		X		X	X	X	
T. pedicellata		X		X			
T. peltata	X	X	X	X	X	X	
T. quadrifida							X
T. sieberi				X		X	
T. tau	X		X	X		X	
T. tetragona						X	

2,000 m. *Tambourissa elliptica* subsp. *elliptica* is a slender, sciaphilous understory forest treelet (1,100–2,000 m). Both species are occasional woody elements of the cloud forest (Fig. 31).

On the tops of exposed crests and at altitudes above ca. 1,700–2,000 m the cloud forest gives way to a low ericoid heath formation dominated by *Philippia,* as in Madagascar and Grande Comore. Apart from the occasional occurrence of *Monimia amplexicaulis, M. rotundifolia, Tambourissa crassa,* and *T. elliptica* subsp. *elliptica,* whose upper ranges end here, no species are specially adapted to the heath formation. Likewise, no species are known to be adapted to the semideciduous dry forest ("forêt mégatherme" of Cadet) in the island's dry, leeward western sector (annual precipitation 800–1,500 mm).

In essence, Réunion's extensive cloud forests have favored adaptive radiation in the genus *Monimia,* which comprises three of its five Monimiaceae species. *Monimia rotundifolia* is the most widespread and abundant species, constituting a woody element of major importance in the cloud forest zone. *Tambourissa,* with two species, has not undergone the extent of adaptive radiation here that has occurred in Mauritius and Madagascar, although seemingly suitable habitats exist. This may be attributable to its more recent arrival, or to the island's younger age. That *Tambourissa* is undergoing adaptive radiation in Réunion is evident by the presence of two closely related species, one with two subspecies occupying different ecological zones.

MAURITIUS

Geologically the oldest of the Mascarene Islands, Mauritius has probably undergone considerable reduction by erosion since its inception, being slightly smaller and only a third as high as Réunion. Since the island's colonization by man almost 400 years ago, its original vegetation has been removed from nearly every accessible surface and has also undergone extreme degradation by introduced biota. Tracts representing most of the island's original vegetion still remain, however, in the form of nature reserves and crown land which comprise ca. 5–6% of its superficies (Lorence, 1978). Unfortunately, virtually all have been invaded by introduced plants such as *Furcraea, Ligustrum, Psidium, Rubus,* and many others, not to mention introduced animals (monkeys, stag, pigs) and birds (sparrows, mynahs, bulbuls), which help spread seeds of the exotic plants. All are contributing to the inevitable disappearance of the remaining native flora and fauna (Vaughan, 1968; Siegfried & Temple, 1975; Jolly, 1982; Pasquier & Jones, 1982).

The majority of forested areas remaining in the uplands (precipitation 2,000–5,000 mm) are occupied by floristically rich wet forest of vari-

able composition but usually characterized by the presence of *Sideroxylon cinereum* Lam., *S. puberulum* A.DC., and other Sapotaceae such as *Labourdonnaisia* (the "*Sideroxylon* thicket" of Vaughan & Wiehe). Remnants of this formation extend down to ca. 200 m in some areas (e.g., at Bel Ombre) where up to three species of *Tambourissa* occur: *T. amplifolia, T. peltata,* and *T. tau* (Table 3; Figs. 38, 40).

In addition to the above, species such as *Tambourissa ficus* and *T. pedicellata* appear at higher altitudes, e.g., at Pieter Both Mt. (Table 3). Vaughan and Wiehe's (1941) detailed study of the *Sideroxylon* formation at Perrier Nature Reserve revealed that two individuals of *Tambourissa peltata* and 16 of *T. tau* occurred in a 1,000 m² plot (Table 4), and family dominance at Perrier was only 0.47%, lowest of the three sites (Table 4). My survey of populations of these two species in the same area shows 26 individuals of *T. peltata* per 12,700 m² (= 21/ha) and 57 individuals of *T. tau* per 512 m² (= 1,113/ha) (Fig. 3). The higher figure for the latter species, an understory treelet, suggests aggregation into much denser populations than *T. peltata,* a more highly dispersed canopy tree. Population density of these two species appears to correspond to their pollinator strategies (see discussion under Floral Biology).

On parts of the upland plateau and in some sheltered valleys the *Sideroxylon* formation passes into a high forest ("climax forest" of Vaughan & Wiehe). Vaughan and Wiehe's (1939, 1941) studies of the high forest at Macabé revealed the presence of 41 individuals 10 cm or more DBH belonging to three species of *Tambourissa* in a one hectare plot. In another 1,000 m² sample plot at Macabé, the genus was found to comprise 2.67% of the total number of individuals 10 cm or more DBH, with the following breakdown: *T. sieberi,* 13 (upper stratum tree); *T. ficus* (as *T. elliptica*), four (mid stratum tree); *T. pedicellata,* 28 (mid stratum tree; my survey in 1979 failed to show this species at Macabé); *T. tau* (as *T. amplifolia*), one (understory treelet). In addition, I found *T. amplifolia* to be a rare understory treelet or small tree at Macabé in 1979 (Table 3).

A comparable survey was carried out in somewhat drier high forest at Brise Fer (Table 3) several kilometers to the west of Macabé (Lorence et al., in prep.). Only two species of *Tambourissa* were found here, *T. ficus* and *T. peltata,* presumably due to the lower rainfall. Both showed up in our study at the rate of two individuals 25 mm or more DBH per 1,000 m².

TABLE 4. Comparative frequency of *Tambourissa* species in three uplant plant formations in Mauritius (adapted from Vaughan & Wiehe, 1941).

Species	Number Individuals per 1,000 m²		
	Philippia Heath (Pétrin)	*Sideroxylon* Wet Forest (Perrier)	Macabé High Forest
T. cordifolia	44	—	—
T. ficus	—	—	4
T. pedicellata	—	—	28
T. peltata	1	2	—
T. sieberi	—	—	13
T. tau	—	16	1
Total	45	18	46
% Family dominance	2.04	0.47	2.67

Because of the island's low altitude, cloud forest only occurs on the flanks and summits of its highest mountains in areas of high rainfall (ca. 4,500–5,000 mm). In their study of the cloud forest (as "mossy forest") on Mt. Cocotte, Vaughan and Wiehe (1937) recorded only two species of *Tambourissa* in a 40 m² transect: *Tambourissa sieberi,* three individuals; *T. tau* (as *T. amplifolia*), two individuals. My survey of the summit of Mt. Cocotte in 1979 (unpubl. data) revealed the presence of five additional species: *Monimia ovalifolia, Tambourissa cocottensis* (endemic to the mountain), *T. ficus, T. peltata,* and *T. tetragona* (also endemic to the mountain) (Table 3). Mt. Cocotte harbors the highest concentration of Monimiaceae in the entire island, with seven of its 11 species found here. A survey of the cloud forest on Mt. Lagrave revealed a comparable situation, with six species present.

Another consequence of the island's low altitude is the paucity of *Philippia* heath formation in Mauritius, which occurs in small patches at only a few edaphically suitable areas such as Pétrin and Mt. Laselle. Formations of this type are restricted to areas of unweathered, highly ferruginous ground water laterite or "cuirasse," so called because of its impermeability to water. Although receiving a high rainfall (4,000 mm at Pétrin), the laterite is nearly devoid of true soil, and the heath formation is exposed to constant drying winds. As a result, most woody species possess xeromorphic leaves (microphyllous, sclerophyllous, or variously pubescent).

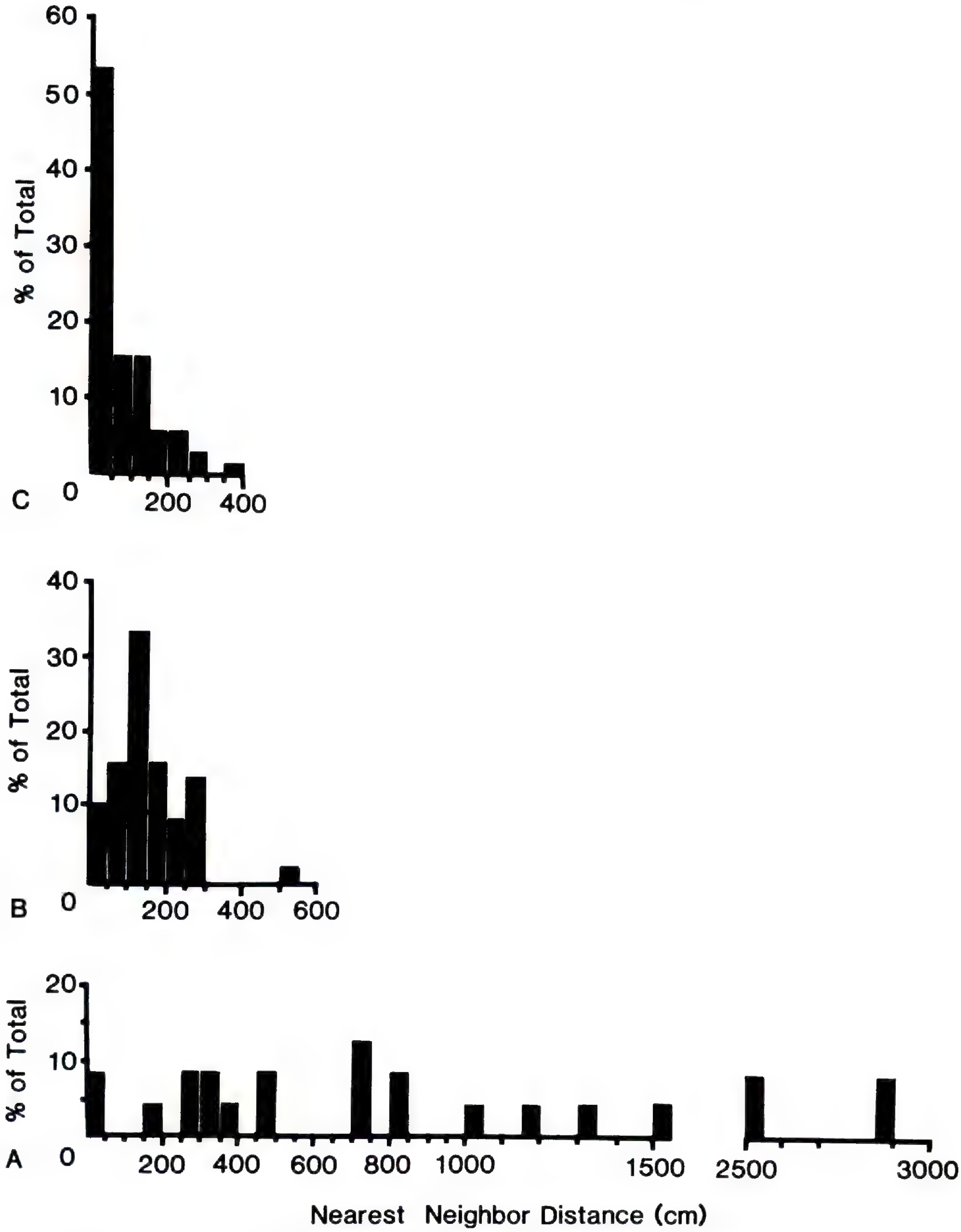


FIGURE 3. Nearest neighbor distance as percent of population for three species of *Tambourissa* studied in Mauritius, 1978–1979.—A. *T. peltata,* Perrier Nature Reserve, sample area = 12,700 m², N = 26 individuals, estimated frequency per hectare = 21.—B. *T. tau,* Perrier Nature Reserve, sample area = 512 m², N = 57 individuals, estimated frequency per hectare = 1,113.—C. *T. cordifolia,* Pétrin Nature Reserve, sample area = 410 m², N = 69 individuals, estimated frequency per hectare = 1,684.

Only a single species of Monimiaceae has successfully adapted to this environment: *Tambourissa cordifolia,* a low dioecious shrub with small, sessile coriaceous leaves. It is peculiar in being the only truly shrubby member of the genus known to me. In their study of a 1,000 m² transect at Pétrin, Vaughan and Wiehe (1941) found 44 individuals of *T. cordifolia.* My study of a population of the species at the same locality gave a much higher density (Fig. 3), 69 individuals per 410 m² (= 1,684/ha), suggesting the species is aggregated into dense, local popula-

tions. *Tambourissa cordifolia* also occurs in a few other regions with similar edaphic conditions, e.g., Mt. Laselle, Les Mares, and Mare Longue Plateau (Fig. 40).

Although *Tambourissa peltata,* and to a lesser degree *T. tau,* also occur in the heath formation at Pétrin, they are only marginally successful and occur as depauperate, stunted individuals. In their 1,000 m^2 sample, Vaughan and Wiehe (1941) only found a single individual of *Tambourissa peltata,* although I found it to be more abundant in localized areas. Family dominance for Monimiaceae in this habitat was 2.04% of the total individuals (Table 4), somewhat less than at Macabé but still a significant element of the woody flora (Vaughan & Wiehe, 1941).

Areas lying to the west of the central plateau, i.e., the western escarpment and lowland areas in the rain shadow (1,000–1,600 mm precipitation), experience a distinct dry season and support a semideciduous dry forest of Mauritius Ebony (*Diospyros tessellaria* Poir.), *Mimusops,* and *Elaeodendron* (Celastraceae). Of the island's ten species of *Tambourissa,* only *T. quadrifida* occupies this habitat to which it is restricted, e.g., at Yemen Valley (Table 3). The species occurs here as a mid stratum or canopy tree often forming small, localized populations.

Although many Monimiaceae readily sprout sucker shoots from cut stumps, no species were found to occur in secondary forests. Furthermore, regeneration of many is poor or lacking even in indigenous forest highly invaded by vigorous exotic species, suggesting that many should be considered as threatened species. For example, on Mt. Cocotte, which is heavily invaded by numerous exotics, only limited regeneration was observed in *Tambourissa ficus* and *T. peltata,* two of the commonest species. No signs of recent regeneration, however, were apparent in the rare and localized *T. cocottensis* and *T. tetragona.* However, vigorous regeneration of both *Tambourissa peltata* and *T. tau* was observed at Perrier Nature Reserve, which has been kept free of exotics for the last decade by a stringent weeding program carried out by the Forestry Department.

In summary, on one hand, Mauritius has favored the greatest adaptive radiation in *Tambourissa* of any of the satellite islands around Madagascar, probably as a result of its comparatively greater age coupled with the availability of a range of suitable habitats. *Monimia,* on the other hand, is represented by a single species confined to the island's few patches of cloud forest. Its poor representation may be attributable to a lack of suitable habitats or a relatively recent introduction.

RODRIGUES

Rodrigues, the smallest, most isolated, and possibly youngest of the Mascarene islands, only attains ca. 400 m maximum elevation and is the least diverse ecologically. As a result of its extreme isolation and paucity of suitable habitats, Monimiaceae appear to be absent from the island (e.g., Balfour, 1879; Wiehe, 1949; J. Guého, pers. comm.). A single collection of *Monimia ovalifolia* supposedly from Rodrigues is probably wrongly labelled (see discussion under the genus *Monimia*).

COMORE ARCHIPELAGO

The Comores are poorly known botanically but appear to harbor predominantly African and Madagascan floristic elements (Voeltzkow, 1917). Of the four islands, information is available only for Grande Comore (Legris, 1969) in the form of a survey of vegetation types and enumeration of their most common and conspicuous elements.

GRANDE COMORE

Grande Comore, youngest of the islands, has virtually no intact lowland forest remaining. Areas of well-developed lower montane wet and montane cloud forest still remain on the lower windward and mid altitude slopes beginning at ca. 500–800 m, however, notably on the Karthala volcano and La Grille massifs where annual precipitation ranges from ca. 3,000 to 5,000 mm (Legris, 1969). Of recent volcanic origin, the La Grille massif supports mature wet forest dominated by large individuals of *Weinmannia, Anthocleista, Eugenia,* and *Macaranga* attaining ca. 20–30 m, and also harbors the island's only species of Monimiaceae, *Tambourissa comorensis.* One of the largest members of the genus, it appears to be restricted to La Grille where it constitutes an important element of the forest, conspicuous because of its numerous large, brown cupuliform fruits hanging from the trunk and major branches (Fig. 17B).

Wet forest on the Karthala volcano massif is dominated by *Ocotea, Nuxia, Olea,* and *Aphloia,* but no Monimiaceae have been noted or collected there to my knowledge. A cloud zone often

forms above ca. 1,000 m. At ca. 1,800–2,000 m the wet/cloud forest zone on Karthala gives way to an ericoid heath formation of *Philippia* similar to that in Madagascar and Réunion; no Monimiaceae are known from this zone.

The leeward western region of the island probably once supported dry forest, of which huge baobabs (*Adansonia digitata* L.) and other scattered trees are the only remnants. No Monimiaceae are known from this zone either.

ANJOUAN

Unfortunately, I was unable to visit Anjouan, which is extremely poorly known botanically. Most of its lowland forest has been destroyed, although the mountainous central massifs (e.g., N'Tingui) support fairly extensive areas of wet and cloud forest due to their rugged relief (I. Tattersall, pers. comm.). Two species of *Tambourissa, T. kirkii* and *T. paradoxa* (syn. *T. johannae*) are known from Anjouan, but little is known of their ecology and distribution. Both apparently occur in the wet and cloud forest zones (Fig. 35). Although Anjouan only attains ca. 1,600 m, it may harbor small amounts of heath vegetation on its highest peaks. Dry forest probably occurred on its dry, lower leeward slopes as is the case for Mayotte and Grande Comore.

MOHÉLI

Mohéli, smallest of the Comores, is also virtually unknown botanically. Although I was unable to visit it, I. Tattersall (pers. comm.) stated that several extensive areas of montane wet forest still remain on its central ridge at Mt. St. Antonio, and between Fomboni and Drondoni (ca. 500–700 m elevation). Collections from these areas made by L. Bernardi in 1967 have revealed the presence of a new endemic species of *Tambourissa, T. moheliensis,* and apparently the only one to occur there. Little is known of its distribution and ecology (Fig. 35). Most of Mohéli's lowland vegetation is now gone. Presumably wet forest occurred on the windward slopes and dry forest on the lower slopes in the rain shadow, as is the case for Mayotte and Grande Comore.

MAYOTTE

Oldest and lowest of the Comores, Mayotte supports only a few small areas of indigenous forest, the rest being cultivated or secondary in nature. Several of the island's highest mountain massifs, i.e., Benara (650 m) and Hachiroungou (500 m), support wet forest dominated by *Nuxia, Aphloia,* and *Macaranga* similar to that found on Grande Comore. Occasional local populations of the Mayotte's only Monimiaceae species, *Tambourissa leptophylla,* still occur here (Fig. 35). A number of large mature individuals and signs of recent regeneration were observed on Benara. *Tambourissa leptophylla* also occurs sporadically as a remnant in wet lowland secondary forest at Barakani and Sada. In the dry, western leeward region remnants of dry forest with *Adansonia digitata* occur on isolated peaks and offshore islets. No Monimiaceae were found to occur there.

In essence, although each of the Comores supports its own single endemic species of *Tambourissa* (two in Anjouan), adaptive radiation of the genus here has been less extensive than in the Mascarenes or Madagascar. As habitat diversity in the Comores is roughly comparable to that in the Mascarenes in spite of their smaller average size, the low *Tambourissa* species diversity may be due to the islands' relative youth or possibly a more recent date of introduction of the genus. That four of the five Comorean species appear to be closely related, and that all species for which data are available are restricted to the wet/cloud forest zone (none are adapted to either dry forest or heath formation), suggests a relatively short history for *Tambourissa* in the Comores.

This review of the ecology and distribution of the Monimiaceae in the Malagasy region demonstrates that members of the family are floristically important constituents of the islands' plant formations. Furthermore, the various species have different life forms ranging from shrubs or understory treelets to mid stratum or even canopy trees. The family attains its greatest diversity and abundance in the lower montane wet and montane cloud forest zones, although a significant number of species are adapted to the lowland wet forest zone. Only a few species are adapted to the high altitude heath formation and the semideciduous dry forest, however. Although many species of *Tambourissa* have the ability to form coppice shoots from cut trunks, they are virtually absent from secondary vegetation and exhibit a poor ability to regenerate when competing with vigorous, invasive exotic species.

Morphology and Anatomy

Because they are generally considered to be a key family for the critical interpretation of a number of other Lauralean families (e.g., Chloranthaceae, Gomortegaceae, Hernandiaceae, and Lauraceae), the Monimiaceae have been relatively well studied morphologically and anatomically (Baillon, 1871; Hobein, 1889; Perkins, 1898, 1925; Perkins & Gilg, 1901; Metay, 1921; Garratt, 1934; Money et al., 1950; Lemesle & Prichard, 1954; Sampson, 1969a, 1969b, 1969c; Endress, 1972, 1980a, 1980b). However, apart from a few species in the genera *Monimia, Tambourissa,* and to a lesser degree *Decarydendron,* the species in the Malagasy area have not been well studied morphologically or anatomically.

METHODS AND MATERIALS

Gross morphological observations were made from herbarium specimens and collections preserved in alcohol. For venation studies, dried leaves were rehydrated, cleared in KOH, bleached, stained in safranin, dehydrated, and mounted in Permount resin between glass plates according to the method of Dilcher (1974). Prints of venation patterns were made using a photographic enlarger and standard photographic print paper (f3, f4, or f5). Leaf trichomes were prepared for the SEM by Au-Pd sputter-coating and photographs were taken on a Cambridge Stereoscan Mark II. Material for floral anatomical studies was fixed in alcohol or FAA (*Monimia,* most *Tambourissa*), or dried herbarium material was restored in 5% NaOH (*Decarydendron, Ephippiandra*) after which it was dehydrated in a TBA series, embedded in Paraplast, sectioned on a rotary microtome, dewaxed and stained with safranin and fast green, and mounted according to methods in Jensen (1962). In some cases, carpels were cleared in KOH, stained, dehydrated, and mounted in Permount to observe the vasculation.

HABIT AND BARK

Monimiaceae in the Malagasy region are mostly understory to mid stratum treelets or small trees, or large canopy trees. I know of no species that occur as emergents. The shrubby habit is quite rare, and no true vines are known from the region. The boles of all species I have observed were cylindric, often with knobby meristematic swellings in the cauliflorous species. The trunk is basally swollen in *Tambourissa ficus, Tambourissa longicarpa,* and *Decarydendron perrieri,* where the flowers are generally produced. None of the species are known to have buttresses or prop roots.

Species of *Monimia* are small- to moderate-sized mid stratum or canopy trees, often shrubby when growing in exposed habitats. Both *M. amplexicaulis* and *M. rotundifolia* reach ca. 10 m tall, whereas *M. ovalifolia* is known to attain 15 m. Trunks of old individuals of all three species are often somewhat reclining and may reach diameters of 30–40 cm in *M. amplexicaulis* and *M. ovalifolia,* and up to 60 cm in *M. rotundifolia.* The bark is generally pale brown or reddish brown, soft, smooth, and flakes off in patches. Because the species are confined to very humid habitats, the bark is often overgrown with bryophytes and other epiphytes.

Of the Madagascan endemic genera, *Decarydendron* and *Ephippiandra* are shrubs, treelets or trees to 10–25 m tall (e.g., *E. madagascariensis* and *E. tsaratanensis*). No information is available on the boles or bark of these two genera.

Tambourissa includes species with a wide range of woody life forms ranging from shrubs rarely exceeding a meter (*T. cordifolia*) to large canopy trees 10–20 m tall (e.g., *T. comorensis, T. sieberi*). The majority of species, however, are understory treelets (e.g., *T. amplifolia, T. tau*) or small mid stratum trees (e.g., *T. ficus, T. purpurea*). The only reportedly vining species is *T. madagascariensis,* a "lianescent shrub" (*Rababoto sub RN 6028,* P), which may also be a large tree 15 m tall (*Anon. sub herb. Alaotra 2126,* MAD). Except for the shrubby *T. cordifolia,* most species are monocaulescent, although many are capable of forming multiple stems from coppice shoots (e.g., *T. cocottensis, T. tau, T. quadrifida*), after death of the main stem.

Although often licheniferous or covered with bryophytes, the bark of most species of *Tambourissa* is pale grayish or brownish, soft and corky, smooth to longitudinally fissured, and flakes or peels off in strips or patches. For the 16 species examined, characteristics of the slash (an oblique cut through the outer and inner bark) include a beige or pale pink to salmon-colored inner bark (phloem), and whitish or straw colored wood (xylem), both showing the conspicuous wide rays characteristic of many Monimiaceae. No sap or exudate was apparent.

In summary, the Malagasy area Monimiaceae

are treelets or trees most abundant in the canopy and lower strata of tropical forests. Only a small number of species have shrubby or lianescent habits. The bark of *Monimia* and many species of *Tambourissa* is relatively uniform, but needs further study in *Decarydendron* and *Ephippiandra*.

WOOD ANATOMY

Anatomical studies of the wood of representative genera and subfamilies of Monimiaceae conducted by Garratt (1934), Money et al. (1950), and Lemesle and Prichard (1954) reveal a number of trends of specialization. Most striking are progressive changes in the vessel members which include a shortening and broadening, a decrease in the degree of end wall overlapping, and a transition from scalariform to simple perforation plates.

Of the four genera examined from the Malagasy area (Money et al., 1950), *Decarydendron, Ephippiandra* (as *Hedycaryopsis*), and *Tambourissa* (all Mollinedioideae sensu Thorne) possess wood anatomical features interpreted as being relatively unspecialized within the family. These include long, thin-walled vessel members with angular, extensively overlapping end walls, and in *Tambourissa* (the only genus for which mature wood was available) scalariform perforation plates (Garratt, 1934; Money et al., 1950).

The xylem of *Monimia* (Monimioideae sensu Thorne) exhibits a number of trends that have been interpreted as advanced within the family (Money et al., 1950). Vessel members of *M. ovalifolia* are relatively short with somewhat obtuse end walls that do not overlap extensively and have perforation plates transitional between scalariform and simple porous. In this respect, specialization in the xylem of *Monimia* (and also *Palmeria*—Mollinedioideae) has attained a level comparable to that of *Peumus* (also Monimioideae), also with simple perforation plates.

Common wood anatomical features shared by both the Monimioideae and the Mollinedioideae are: scanty wood parenchyma; rather broad, multiseriate rays; presence of septate fibers; presence of fibers and hippocrepiform sclerids in the stem pericycle (Money et al., 1950).

STEMS AND PHYLLOTAXY

Adult phyllotaxy in *Monimia, Decarydendron, Ephippiandra,* and most species of *Tambourissa* is opposite to subopposite and decussate. The three *Tambourissa* species in species Group 8 have ternate to subalternate adult leaves (Table 1), although seedlings of two, *T. ficus* and *T. peltata,* have opposite decussate leaves. On the other hand, adult leaves of species which are normally opposite are sometimes ternate on vigorous sucker shoots (e.g., *Monimia ovalifolia, Tambourissa purpurea,* and *T. pedicellata*). Although opposite and decussate, the adult leaves of *T. tau* (Fig. 39A) are unique in being clustered into pseudoverticels of two to four pairs, separated by long "internodes." Phyllotaxy is generally a constant, species-specific feature.

Leafy stems of most species of all four genera are more or less terete with flattened, somewhat dialated nodes. *Tambourissa tetragona* is unique in having winged, quadrangular stems, whereas those of the ternate leaved species (Group 8) are somewhat trigonous.

Stems of *Decarydendron, Ephippiandra,* and most *Tambourissa* species bear sparse to dense, straight or undulate, simple or rarely fasciculate (e.g., *T. comorensis, T. mohelensis*) lignified trichomes. In a few species even the new growth is virtually glabrous (e.g., *T. cocottensis, T. cordifolia,* and *T. tetragona*). In *Monimia,* the stems are scabrous to velutinous with an indument of stellate, fasciculate and simple trichomes. Lenticels often occur on the stems of certain species (e.g., *T. ficus, T. peltata, E. perrieri, E. domatiata,* and *E. myrtoidea*) but are absent in most. Stem characters thus provide a number of species-specific, taxonomically useful features.

Monimia, Decarydendron, Ephippiandra, and *Tambourissa* all characteristically possess multiple axillary buds of which I found no mention in the literature. In all three species of *Monimia* (as in *Peumus*), three horizontally oriented buds are usually present in each leaf axil, the central one being largest and developing first (if at all). The vegetative buds have small, pubescent scales, whereas those enclosing the inflorescence are large, brown, and subglabrous. In the remaining genera, all Mollinedioideae, the buds are oriented longitudinally in the leaf axil, the central one usually being largest and the first to develop (if at all). On flowering branches of the ramiflorous species *E. madagascariensis* and *E. tsaratanensis* there are three to five buds, the central one usually giving rise to the inflorescence and the lateral ones to vegetative shoots. In *D. helenae* var. *stenophyllum* the buds occur in groups of three, whereas in *E. microphylla* and *E. myrtoid-*

ea they are solitary or in pairs. Three, less commonly two, axillary buds are present in nearly all species of *Tambourissa* examined, regardless of whether the inflorescence is terminal, ramiflorous or cauliflorous. On flowering stems of ramiflorous species such as *T. purpurea,* the large central bud frequently but not invariably gives rise to the inflorescence. On vegetative stems, the central bud usually develops first, although two buds may occasionally develop into vegetative shoots simultaneously. *Tambourissa tetragona* is exceptional in that only one bud is obvious. However, vigorous sucker shoots of *T. ficus* may produce up to six buds extending in a row for several centimeters above the leaf axil (*Lorence 2235,* MO).

LEAVES

The terminology used to describe leaves in this monograph follows Hickey (1973, 1977), Hickey and Wolfe (1975), and to an extent Lawrence (1951). Leaves of all Monimiaceae are exstipulate, considered by Hickey and Wolfe (1975) to be an advanced condition within the Laurales. Characters of the petiole and lamina, including size and shape, margin, venation, and pubescence, provide a series of taxonomically useful features in many taxa.

Petiole. The leaves of most genera and species have a well-differentiated lamina and petiole, but *Monimia amplexicaulis* (Fig. 4A) and *Tambourissa cordifolia* (Fig. 8B) are unique in having sessile cordate, amplexicaul leaves. Petioles of most other species are slender to stout, of variable length but much shorter than the lamina, and are adaxially flattened or canaliculate. They are either glabrous or bear an indument of trichomes similar in type and density to that of the stem internodes. In all three species of *Monimia* (*M. amplexicaulis, Lorence 2503,* MO; *M. ovalifolia, Lorence 1857,* MO; *M. rotundifolia, Lorence 2472,* MO), the vascular strands of the petiole are united into an adaxially flattened cylinder (see also Money et al., 1950). In the other genera which I examined (*Ephippiandra myrtoidea, Baron 1355,* K; *E. madagascariensis, Bernardi 11977,* MO), and six species of *Tambourissa* (*T. cocottensis, Lorence 2287,* MO; *T. crassa, Lorence 2767,* MO; *T. elliptica* subsp. *micrantha, Lorence 2488,* MO; *T. ficus, Lorence 2162,* MO; *T. pedicellata, Lorence 2385,* MO; and *T. tetragona, Lorence 2286,* MO), the petiolar vascular strands are aggregated into a shallow, U-shaped arc. This corresponds with Metay's (1921) findings for *T. floricostata* (as *Schrameckia madagascariensis*) and *T. thouvenotii.*

Lamina. Leaves of *Monimia* are subcoriaceous to coriaceous, usually ovate to elliptic or suborbiculate, and their size and shape are generally much more polymorphic in *M. ovalifolia* and *M. rotundifolia* than in *M. amplexicaulis.* Although the extreme forms appear to be very distinct (Fig. 4), leaf size and shape in *Monimia* do not provide stable taxonomic features. Likewise, shape of the apex is quite variable (acuminate, acute, or obtuse) and of little taxonomic importance in all three species. Characters of the leaf base, however, are useful in distinguishing *M. amplexicaulis,* where it is deeply cordate and amplexicaul, from the other two species where it ranges from shallowly cordate to rounded, obtuse, acute or decurrent (Fig. 4).

Leaves of the three species of *Decarydendron* do not differ markedly from each other, ranging from elliptic to oblong or obovate. The texture is chartaceous to subcoriaceous, the apex acute or acuminate, and the base cuneate.

Leaves of the six species of *Ephippiandra* are small- to medium-sized and chartaceous to coriaceous in texture. Laminar shape is generally characteristic for each species: ovate or elliptic with acute or acuminate apices and cuneate to rounded bases in *E. microphylla* and *E. myrtoidea* (Fig. 6A); elliptic with a retuse apex folded downward into a flap in *E. perrieri* (Fig. 6B); obovate-elliptic to rhombic and apiculate in *E. domatiata*; orbicular with an obtuse to truncate base and obtuse to rounded apex in *E. madagascariensis* and *E. tsaratanensis.* (Fig. 6E, F).

The 43 species of *Tambourissa* display a wide array of leaf morphologies which are relatively constant and species-specific. In widespread species with a broad ecological amplitude (e.g., *T. peltata, T. purpurea*), considerable intraspecific variation occurs in size and shape, generally between populations growing in different habitats. Texture ranges from membranaceous in *T. leptophylla* to coriaceous in *T. parvifolia* and *T. religiosa.* Size varies from small in *T. parvifolia* (attaining only 47 mm by 22 mm) which grows in high altitude montane forest, to very large in *T. amplifolia* (attaining 500 mm by 240 mm) which grows in lowland wet forest. Leaf shape varies considerably within many species but in others it is of considerable taxonomic significance, e.g., in distinguishing the two subspecies of *T. elliptica.* Leaf shape in the genus ranges

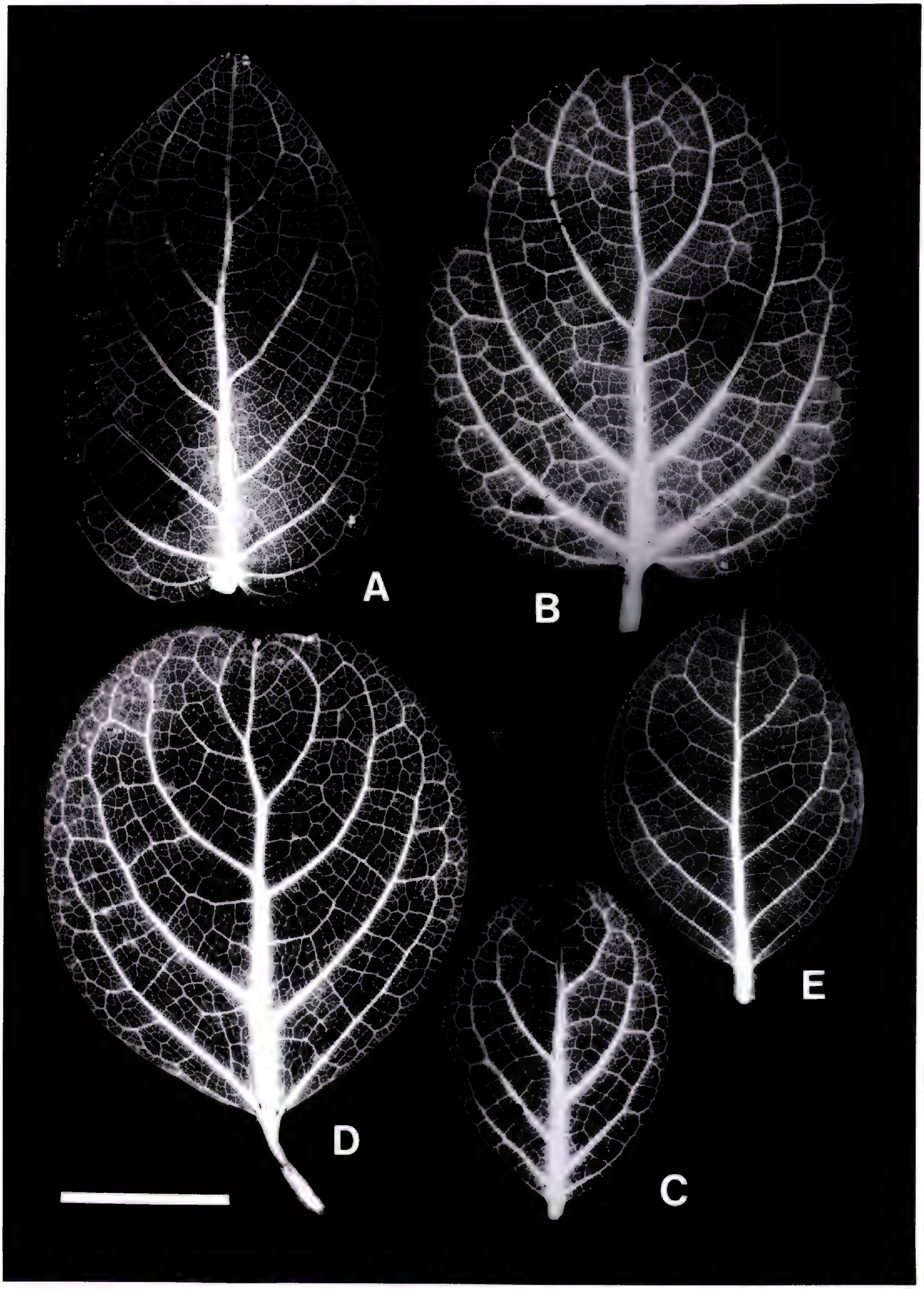


FIGURE 4. Leaf clearings of *Monimia*.—A. *M. amplexicaulis, Rivals s.n.* (TL-R).—B. *M. rotundifolia, Rivals s.n. in June 1943* (TL-R).—C. *M. rotundifolia, Bosser 21332* (P).—D. *M. ovalifolia, Cordemoy s.n.* (TL-R).—E. *M. ovalifolia, Guého sub MAU 14130* (MAU). Bar equals 25 mm.

from cordate or ovate to elliptic, oblong, or obovate.

Studies of leaf anatomy in *Monimia* and *Tambourissa* (Hobein, 1889; Metay, 1921) show their laminar structure to be similar to that of many bifacial dicot leaves. The two species of *Monimia* and six species of *Tambourissa* examined by them all have a cuticle, an upper epidermis, a hypodermis consisting of one to six cell layers, a mesophyll differentiated into a palisade layer one or two cells thick and a spongy layer many cells thick, and a lower epidermis also covered by a cuticle. Stomata are restricted to the lower epidermis in all species except *T. thouvenotii,* which also has stomata in the upper epidermis (Metay, 1921).

Leaves of Monimiaceae are characterized by the presence of spheroid laminar glands or secretory cells containing so-called "ethereal" oils which impart a particular odor to many species. In most species of *Tambourissa* these are concentrated in the mesophyll, but lesser numbers also occur in the lower epidermis and hypodermis (Hobein, 1889; Metay, 1921). Hobein (1889) stated that both *Monimia ovalifolia* and *M. rotundifolia* have secretory cells restricted to the hypodermis and not in the mesophyll as in *Tambourissa* and the other genera he studied. My investigations of hand sectioned, alcohol fixed leaves show that secretory cells are restricted to the hypodermis only in *M. ovalifolia,* both in plants from Mauritius (*Lorence 1857, 2896,* MO) and from Réunion (*Lorence 2757,* MO). In *M. amplexicaulis* (*Lorence 2503,* MO) and *M. rotundifolia* (*Lorence 2472,* MO), secretory cells were found to occur not only in the hypodermis, but also in the interface between the palisades and spongy mesophyll. An examination of sections of restored leaves of *Decarydendron helenae* var. *stenophyllum* (*Humbert 6613,* K), *Ephippiandra tsaratanensis* (*Gentry 11605,* MO), and *E. myrtoidea* (*Baron 1263,* K) shows that they are fundamentally similar to species of *Tambourissa* anatomically.

Venation and margin. The Monimiaceae possess several distinctive trends which Hickey and Wolfe (1975) consider to be advanced within the Laurales, notably development of the Monimioid tooth with an unbraced medial vein and an indurated cap, and secondary veins originating at uniform angles to the costa.

All three species of *Monimia* possess stoutly brochidodromous venation of the festooned type characteristic of the family. Three to four pairs

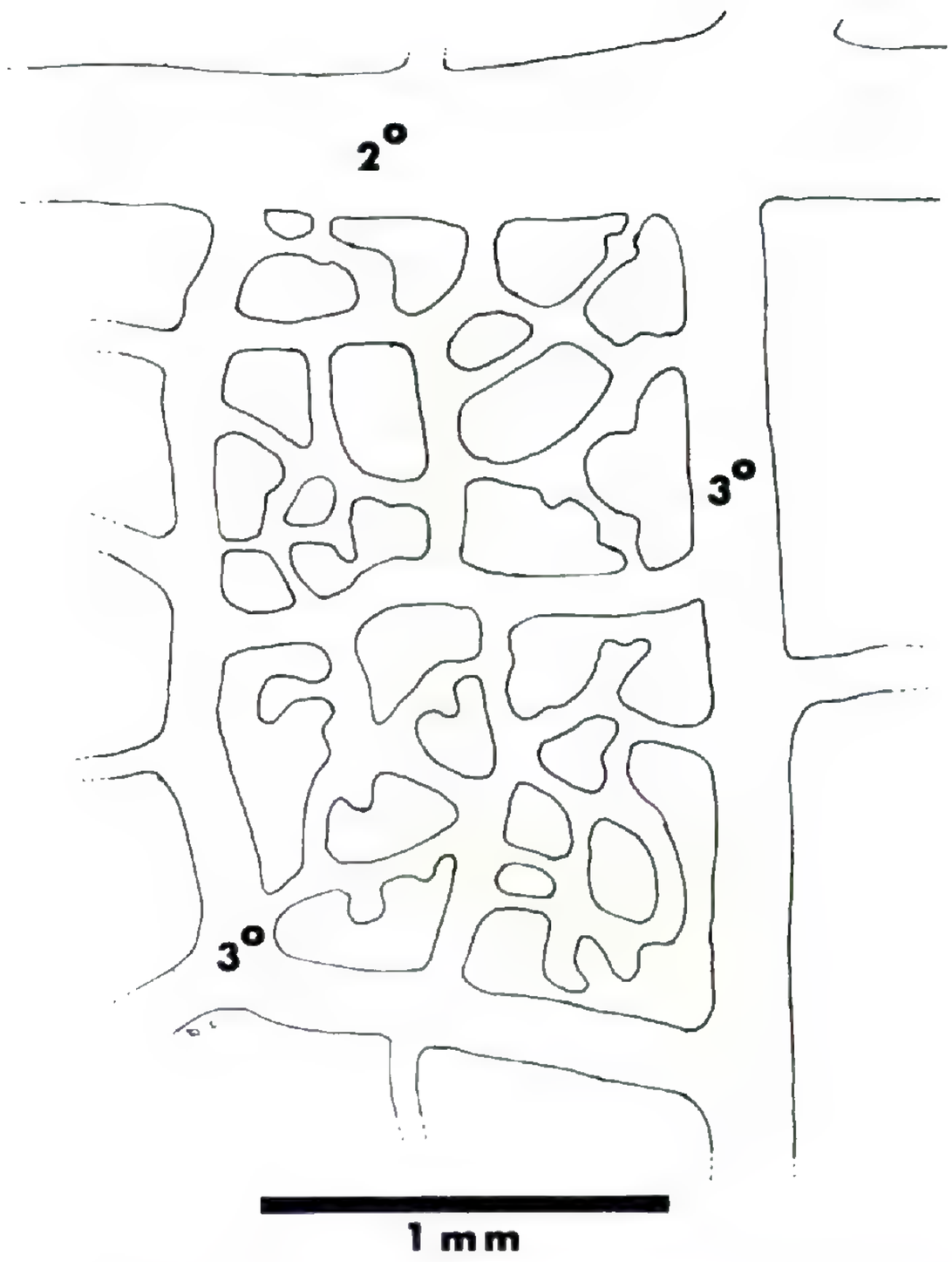


FIGURE 5. Camera lucida drawing of ultimate venation in cleared leaf of *Monimia ovalifolia, Bijoux sub MAU 1310* (MAU). 2° = secondary venation, 3° = tertiary venation.

of secondary veins originate at comparatively uniform angles, are bowed to geniculate, follow a regular, slightly sinuous course and delimit relatively regular and uniform intercostal areas (Fig. 4A–E). Consequently, all three species fall into Hickey's (1977) second rank leaf category. Distally the secondaries continue to form another, higher order of loops characteristic of the festooned brochidodromous venation pattern (Hickey & Wolfe, 1975). The numerous intermarginal loops of the last order unite to form a weak, fimbriate intramarginal vein generally lacking in the other genera.

Intercostally, the tertiary veins originate at right angles from the secondaries and their arches and unite to form a series of strong, transverse tertiaries which in turn ramify at right angles and then anastomose admedially to form composite intersecondaries that usually follow a zig-zag course. These tertiary areoles are generally orthogonal (rectangular or pentagonal) and much more regular than in the other genera (Figs. 4, 5). The quaternaries arise from the tertiaries at nearly right angles to form fairly regular rectangular areoles. Vein orders above the quater-

nary are generally indistinct and ramify to form a reticulum of irregular areoles with included veinlets that anastomose or remain free (Fig. 5). Terminal idioblasts appear to be absent from the veinlets. The number and pattern of veins in *Monimia* provide few characters useful in separating the species, although they are characteristic of the genus as a whole.

Adult leaves of all three *Monimia* species have entire, generally slightly revolute margins. Seedling leaves of *M. ovalifolia* and *M. rotundifolia* (unknown in *M. amplexicaulis*) are also entire, as opposed to those of *Tambourissa* (D. Lorence, pers. observ.) and *Hortonia* (Endress, 1980a) which are generally dentate. Although the Monimioid tooth is, ironically, absent in *Monimia,* its venation is highly organized and appears to be advanced in this respect. The genus may possibly have undergone loss of teeth secondarily, as appears to be the case for *Tambourissa.*

Venation in all three species of *Decarydendron* is festooned brochidodromous. The six to 12 pairs of secondaries arise at quite constant angles, delimit regular intercostal areas, and continue to loop for several orders. Tertiary veins arising inside the secondary arches ramify admedially to form a reticulum of irregular areoles as they descend obliquely across the intercostal area. The quaternaries arise from the tertiaries at irregular angles and delimit irregular areoles. Vein orders above the quaternary are indistinct, and probably ramify to form free, included veinlets. Adult leaves of all three species of *Decarydendron* are serrate-dentate along the greater portion of their plane margins, each tooth ending in an indurated cap. An unbranched distal excurrent vein arising from the outer series of brochidodromous arches runs directly into each tooth. In this respect the venation is not truly semicraspedodromous according to Hickey's (1973) definition.

Species of the genus *Ephippiandra* (including *Hedycaryopsis*) display a distinctive trend from festooned brochidodromous to specialized and highly organized semicraspedodromous and craspedodromous patterns, the latter unknown elsewhere in the family. Leaves of *E. microphylla, E. myrtoidea,* and *E. perrieri* are small with only four to six pairs of secondary veins which unite into arches near the margin, and the festooning is often weak (Fig. 6A, B). Several tertiary veins arise on the distal parts of the secondary arches and descend parallel to the secondaries or somewhat obliquely across the intercostal areas, often ramifying into strongly admedial branches as they approach the costa. The tertiaries delimit irregular intercostal areas in *E. myrtoidea,* but these are more regular and orthogonal in *E. perrieri.* Higher vein orders above the tertiary are not very distinct and generally form a more or less random reticulum of irregular areoles, ultimately terminating in free, dendroid veinlets lacking idioblasts. Margins are entire and somewhat revolute in *E. myrtoidea* and *E. perrieri,* but those of *E. microphylla* generally have a single pair of small teeth in the apical portion arising from exmedial branches of the secondary arches.

Leaves of *E. domatiata* (Fig. 6C, D) are likewise small with two to three pairs of secondaries, but show certain modifications towards the semicraspedodromous pattern. Although the weak basal pair of secondary veins forms a series of festooned loops in the customary brochidodromous manner, the second, stronger pair ascends for over half the lamina's length before joining the next pair above. On each side of the lamina one of the secondary branches runs directly into the margin, terminating in a small tooth. The tertiaries delimit fairly irregular intercostal areas, although the quaternaries form more regular areoles with free, branching veinlets. The margin is moderately revolute, and it is the only species known to have barbate domatia in the basal secondary vein axils, hence the specific epithet.

Ephippiandra tsaratanensis (Fig. 6E) has much larger, broader leaves which show a weakening of the brochidodromous pattern and the formation of sunken marginal teeth. As each of the four to seven pairs of secondary veins bifurcates, each branch generally unites with an adjacent branch to form a weak arch whose exmedial portion in turn gives rise to one or more distal branches. Each of these runs to the margin where it terminates in a rounded, centrally depressed tooth. The intersecondary webbing pattern of the tertiaries is stronger than in the preceding species, with more regular orthogonal, often quadrangular, tertiary areoles frequently bisected by zigzagging admedial branches. The quaternaries form generally small, more or less orthogonal areoles with free, included branched veinlets.

Leaves of the sixth species, *Ephippiandra madagascariensis* (Fig. 6F) are the most highly specialized of all, being almost orbicular with four to five pairs of secondary veins forming an open, craspedodromous pattern due to a further weakening of the secondary arches. Each secondary departs from the costa at a uniform angle

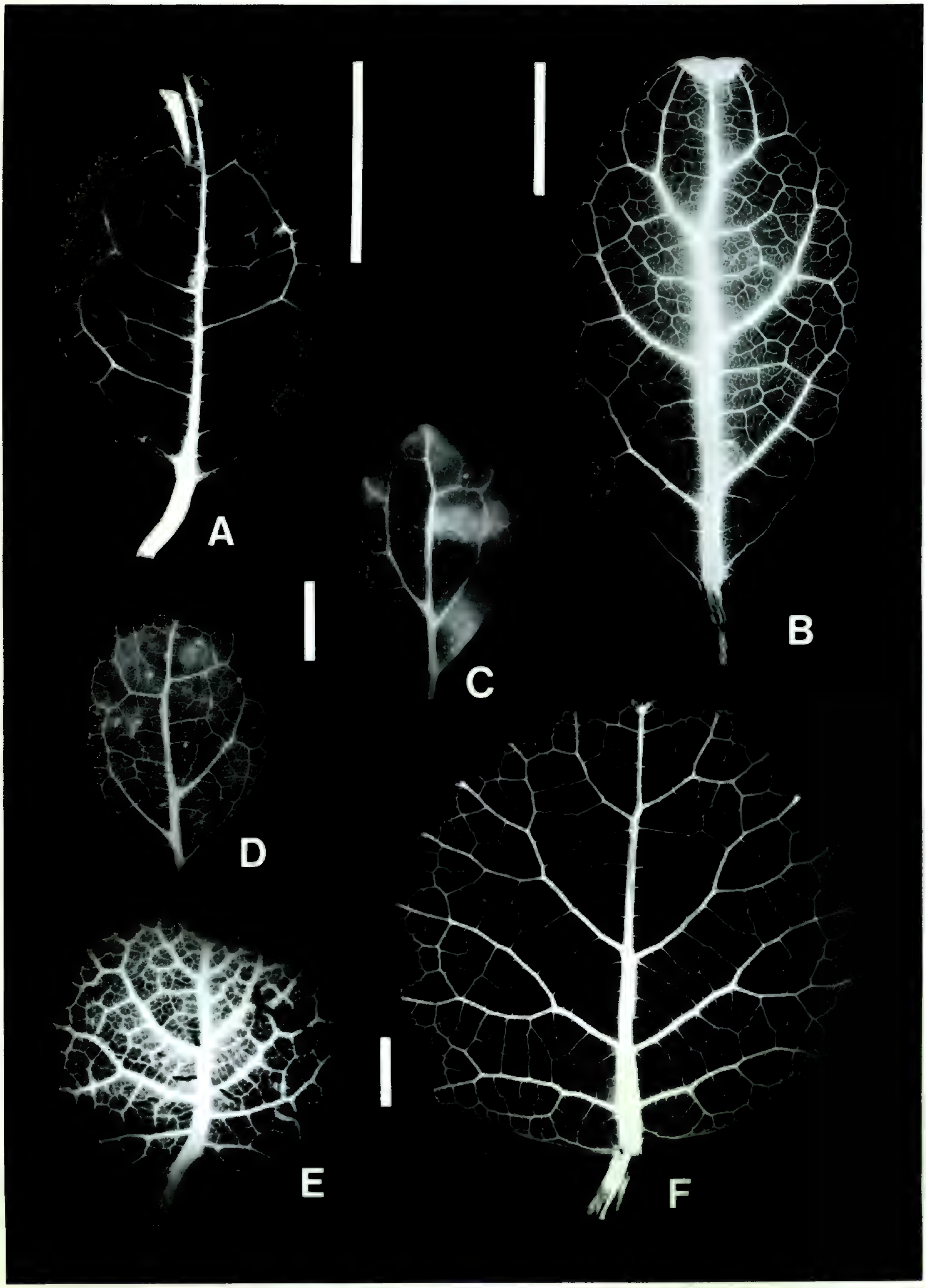


FIGURE 6. Leaf clearing of *Ephippiandra*.—A. *E. myrtoidea, Baron 1355* (K).—B. *E. perrieri, Morat 2332* (MAD).—C, D. *E. domatiata, Capuron 8828-SF* (P).—E. *E. tsaratanensis, Gentry 11605* (MO).—F. *E. madagascariensis, Bernardi 11977* (MO). Bars equal 10 mm.

and generally bifurcates once or rarely twice before the (usually basal) branch terminates in a single, depressed tooth as in the previous species. Occasionally, an apical sub-branch unites with a superadjacent secondary. As in the latter species, the tertiaries form a strong intersecondary cross webbing pattern delimiting regular intercostal areas. The tertiaries nearest the costa frequently display a strongly admedial zigzag branching pattern, whereas the quaternaries generally form irregular areoles with highly branched, free included veinlets as in the other species. The margin of *E. madagascariensis* is sinuate-dentate with seven to nine pairs of sunken teeth, including one at the apex, as in the preceding species. These teeth contain terminal tracheary elements and appear to be hydathodal.

A situation analogous to that in *Ephippiandra* occurs in *Hibbertia* (Dilleniaceae). Rury and Dickison (1977) explain the ontogenetic transitions in *Hibbertia* as follows:

> "The craspedodromous venation pattern appears to be (in most cases) the result of an ontogenetic modification of the weakly brochidodromous pattern. Semicraspedodromous venation apparently resulted from formation and subsequent vascularization of marginal teeth in leaves with weakly brochidodromous venation. The tooth vasculature arises exmedially from the brochidodromous arch in leaves of *Hibbertia cuneiformis,* etc."

This same transition is apparent in the six species of *Ephippiandra*: a weakening and opening of the brochidodromous pattern with subsequent vascularization of the teeth from the secondary branches. This transition from weak brochidodromy to simple craspedodromy could result from a differential thickening of the portion which connects the basal part of the secondary arch with the marginal tooth, which can be seen in the basal veins of *E. madagascariensis.* According to Rury and Dickison (1977), Hickey (pers. comm.) stated that the ontogenetic transition from semicraspedodromy to simple craspedodromy has resulted from such a shift in vein development in many dicot leaves.

Tambourissa species (including *Phanerogonocarpus*) have venation patterns based on the festooned brochidodromous theme. Number of secondary veins ranges from three or four pairs (e.g., *T. parvifolia,* Fig. 8C; *T. elliptica* subsp. *elliptica,* Fig. 7D; *T. thouvenotii,* Fig. 7A), to six to 12 pairs in *T. elliptica* subsp. *micrantha* (Fig. 7E). The secondaries are stout, straight or sinuate, and delimit intercostal areas which may be irregular (*T. thouvenotii,* Fig. 7A), or quite regular (*T. elliptica* subsp. *micrantha,* Fig. 7E; *T. cordifolia,* Fig. 8B). Species with fewer secondary veins frequently have less regular intercostal areas; some of these approach Hickey's (1977) "first rank" leaf category in this respect (e.g., *T. thouvenotii,* Fig. 7A). The majority of species, however, fall into his "second rank" category. In these, the secondaries from a fairly strong series of brochidodromous arches and continue to loop or festoon for several orders. The ultimate exmedial series of loops is often irregular and discontinuous (e.g., *T. leptophylla,* Fig. 8E), and does not form a true marginal fimbrial vein, although the strong intramarginal loops of *T. religiosa* resemble a fimbrial vein (Fig. 8D). The tertiary veins arise at wide acute to slightly obtuse angles from the secondaries and their arches, and are often admedially and obliquely ramified, forming strong, composite intersecondaries (e.g., *T. elliptica* subsp. *micrantha,* Fig. 7E). Tertiary areoles are generally irregular, although orthogonal areoles may be delimited by transverse tertiaries in some species with more highly organized venation (e.g., *T. peltata,* Fig. 8A; *T. elliptica* subsp. *elliptica,* Fig. 7D). Higher order veins are generally indistinct above the quaternary and sometimes tertiary levels. The quaternaries generally ramify and anastomose to form irregular areoles with dendroid, highly branched, free included veinlets. Terminal idioblasts are absent.

The margins of adult leaves of the majority of *Tambourissa* species are entire and plane to revolute. Exceptional are *T. thouvenotii, T. trichophylla,* and the two species formerly included in *Phanerogonocarpus,* i.e., *T. alaticarpa* and *T. longicarpa.* The former two possess half-toothed leaves with one to eight pairs of Monimioid teeth in the apical portion of the lamina. In *T. trichophylla* (Fig. 7C), the secondary arches are strong and delimit low, broad intercostal areas, with an excurrency of the secondary arch running into each tooth. The apical portion of the lamina is therefore semicraspedodromous. In *T. thouvenotii* (Fig. 7A), the secondaries delimit high, narrow intercostal areas and the arches are much weaker, approaching the semicraspedodromous pattern of *Ephippiandra.* In some leaves of *T. thouvenotii* the main, apical secondary branch runs directly into the tooth, and any festooning is very weak. In others, it more closely resembles the pattern in *T. trichophylla.*

Leaves of the two species formerly included in *Phanerogonocarpus* (*T. alaticarpa* and *T. lon-*

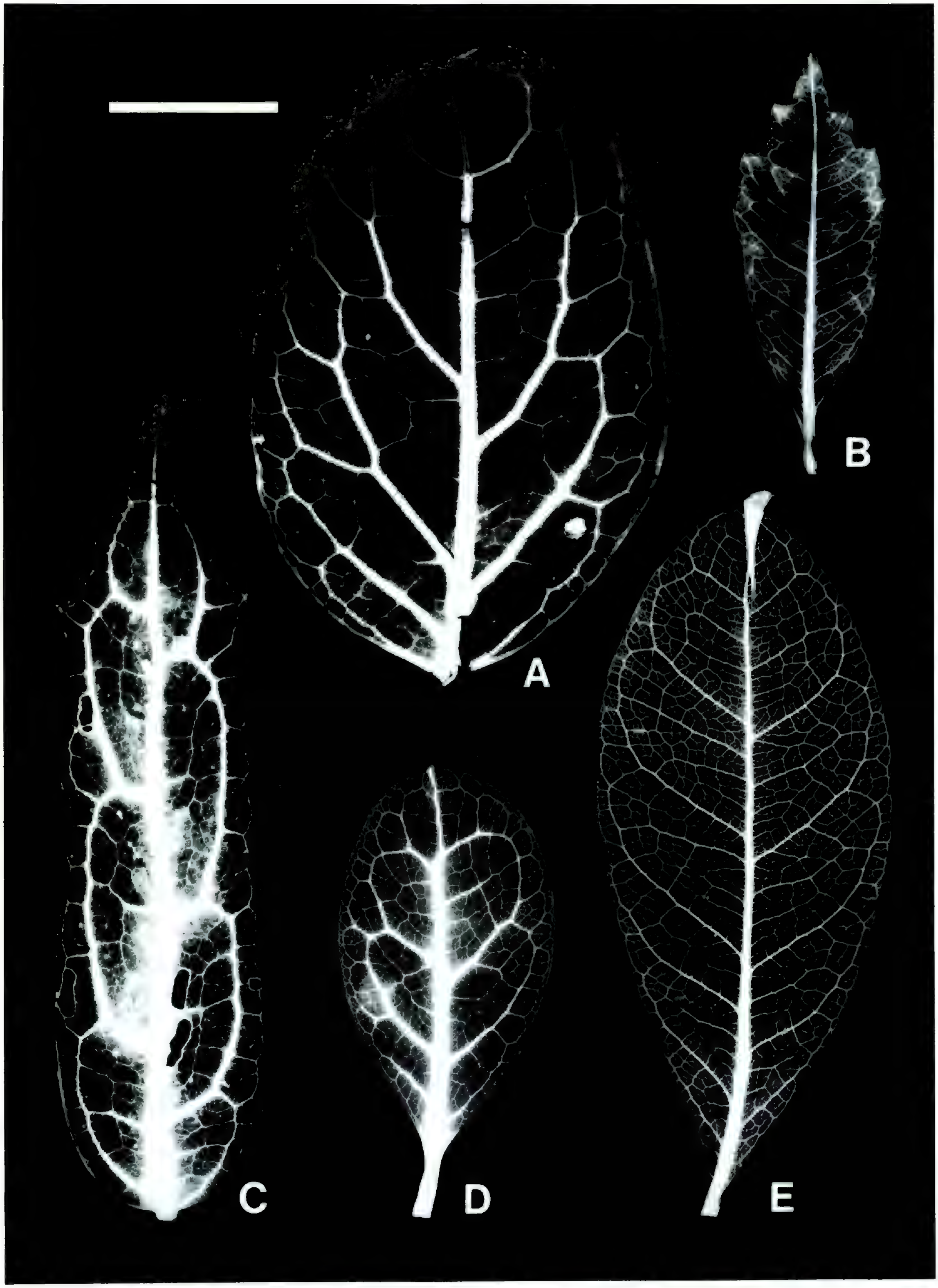


FIGURE 7. Leaf clearings of *Tambourissa*.—A. *T. thouvenotii, Thouvenot s.n. in 1919* (BM).—B. *T. ficus,* juvenile from sucker shoot, *Richardson 4042* (K).—C. *T. trichophylla, Lorence 1879* (MO).—D. *T. elliptica* subsp. *elliptica, Friedmann 2299* (P).—E. *T. elliptica* subsp. *micrantha, Coode 4956* (K). Bar equals 25 mm.

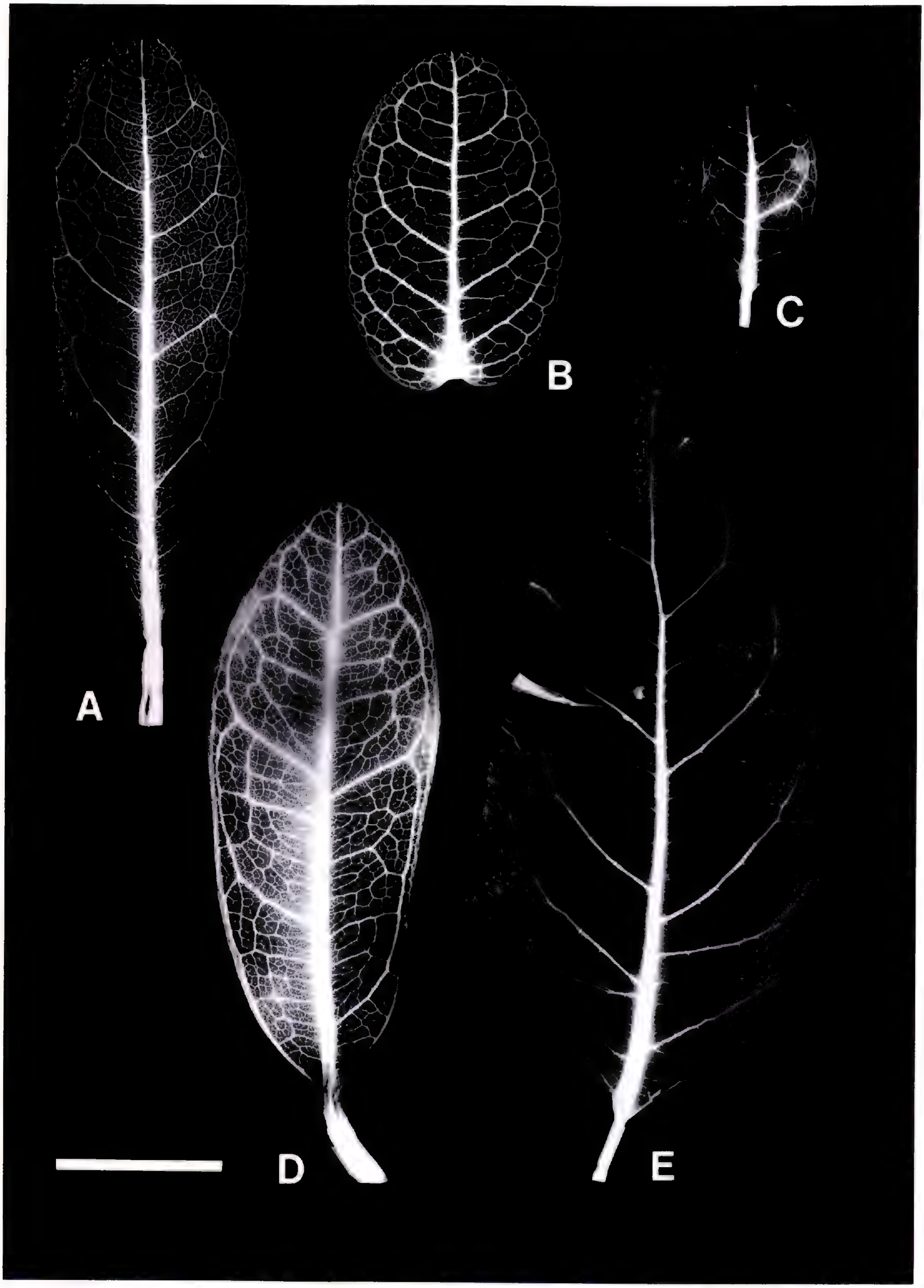


FIGURE 8. Leaf clearings of *Tambourissa*.—A. *T. peltata, Guého sub MAU 12543* (MAU).—B. *T. cordifolia, Lorence M 144* (MO).—C. *T. parvifolia, Baron 4204* (K).—D. *T. religiosa, Decary 6554* (P).—E. *T. leptophylla, Tattersall s.n.* (MO). Bar equals 25 mm.

gicarpa) have five to eight pairs of secondary veins arising at quite uniform angles which delimit fairly regular intercostal areas and unite in a festooned brochidodromous pattern. In *T. alaticarpa,* the apical ⅔–¾ of the margin is dentate with eight to ten pairs of slender, antrorse teeth (Fig. 17A). That of *T. longicarpa* is broadly dentate with two or three pairs of large teeth in the apical ⅓–½ of the lamina. In both, the teeth arise from exmedial branches of the secondary or tertiary arches, thus rendering the venation semicraspedodromous.

In the context of Rury and Dickison's (1977) findings for *Hibbertia* where teeth develop in the adult leaves, it would seem that the dentate species of *Tambourissa* are advanced within the genus. My field studies show, however, that seedlings of virtually all species of *Tambourissa,* which I have seen, produce apically dentate leaves. This condition frequently also occurs on sucker shoots (e.g., *T. ficus,* Fig. 7B) where they are gradually lost in the ontogenetic transition to entire adult leaves. These *Tambourissa* species therefore appear to lose their teeth secondarily, as also occurs in *Hortonia* (Endress, 1980a). In this context, the four dentate species may represent cases of neoteny. This does not, however, contradict Hickey and Wolfe's (1975) suggestion that the Monimoid tooth is an advanced feature within the family.

TRICHOMES

Apart from the three virtually glabrous *Tambourissa* species mentioned above, stems and leaves of most species in all four genera bear at least some trichomes. Leaf pubescence ranges from a few scattered hairs along the petiole and major veins, to the entire lamina being canescent or velutinous-tomentose. Stem pubescence is comparable to that of the leaf. Trichomes of all the genera examined are nonglandular, lignified (e.g., stain pink or red with phloroglucinol; Hobein, 1889), and are simple and unicellular (except in *Monimia*). In a few *Tambourissa* species they are fasciculate, i.e., grouped into clusters of two or three.

Three types of trichomes occur in *Monimia*: long, unicellular; multicellular, fasciculate consisting of two to eight long, ascendent, unicellular arms united basally to form the stalk; short, appressed, multicellular stellate or stellate-peltate composed of six to 16 horizontal arms radiating from a common center and joined basally to form the stalk. Trichome density is greatest on the abaxial laminar surface where they form a thick, whitish indument completely obscuring the leaf surface (Fig. 9E), whereas they are scattered and more easily distinguished on the adaxial surface. Trichomes play a key role in distinguishing the three species of *Monimia. Monimia ovalifolia* is distinct in having small, appressed, stellate-peltate trichomes with six to 16 short arms united basally for ⅓–½ their length (Fig. 9D, E), a character shared by populations both from Mauritius and Réunion. In addition to stellate trichomes with fewer long, free arms, *M. amplexicaulis* and *M. rotundifolia* also have simple and fasciculate trichomes (Fig. 9A–C). Although both the latter species may display considerable variation in trichome composition, even within a single population, they are modally distinct.

In the Mollinedioideae, *Ephippiandra domatiata, E. madagascariensis, E. microphylla, E. myrtoidea,* and *E. perrieri* are all sparsely pubescent or subglabrous with short, pale simple trichomes, whereas *E. tsaratanensis* is easily distinguished by its long, dense simple reddish trichomes. Trichomes of *Decarydendron* are simple, yellowish, and generally longer than in *Ephippiandra.* Leaf pubescence in *Tambourissa* ranges from completely glabrous in a few species (e.g., *T. cocottensis, T. tetragona,* species Group 5), to subglabrous (e.g., *T. tau,* species Group 5), canescent or villous in many (e.g., *T. nosybensis, T. hildebrandtii,* species Group 1B), or even densely velutinous-tomentose in a few (e.g., *T. thouvenotii, T. trichophylla,* species Group 1A; *T. longicarpa,* species Group 8). Trichomes therefore constitute a taxonomically useful character in the Monimiaceae.

INFLORESCENCE

Inflorescence structure in the four genera is quite variable: thyrsic, cymose (pleiochasial, dichasial, or monochasial), fasciculate, or solitary. Although more than one inflorescence type frequently occurs within a given species, and often on a single individual, the inflorescence generally provides a taxonomically useful suite of characters. Flowers of all the genera and species in this study are unisexual, and sexual makeup of the inflorescence is often stable and characteristic. For example, *Monimia* is invariably dioecious, although sex expression in the other taxa is often more variable. Inflorescence position varies greatly within the genera, but is frequently

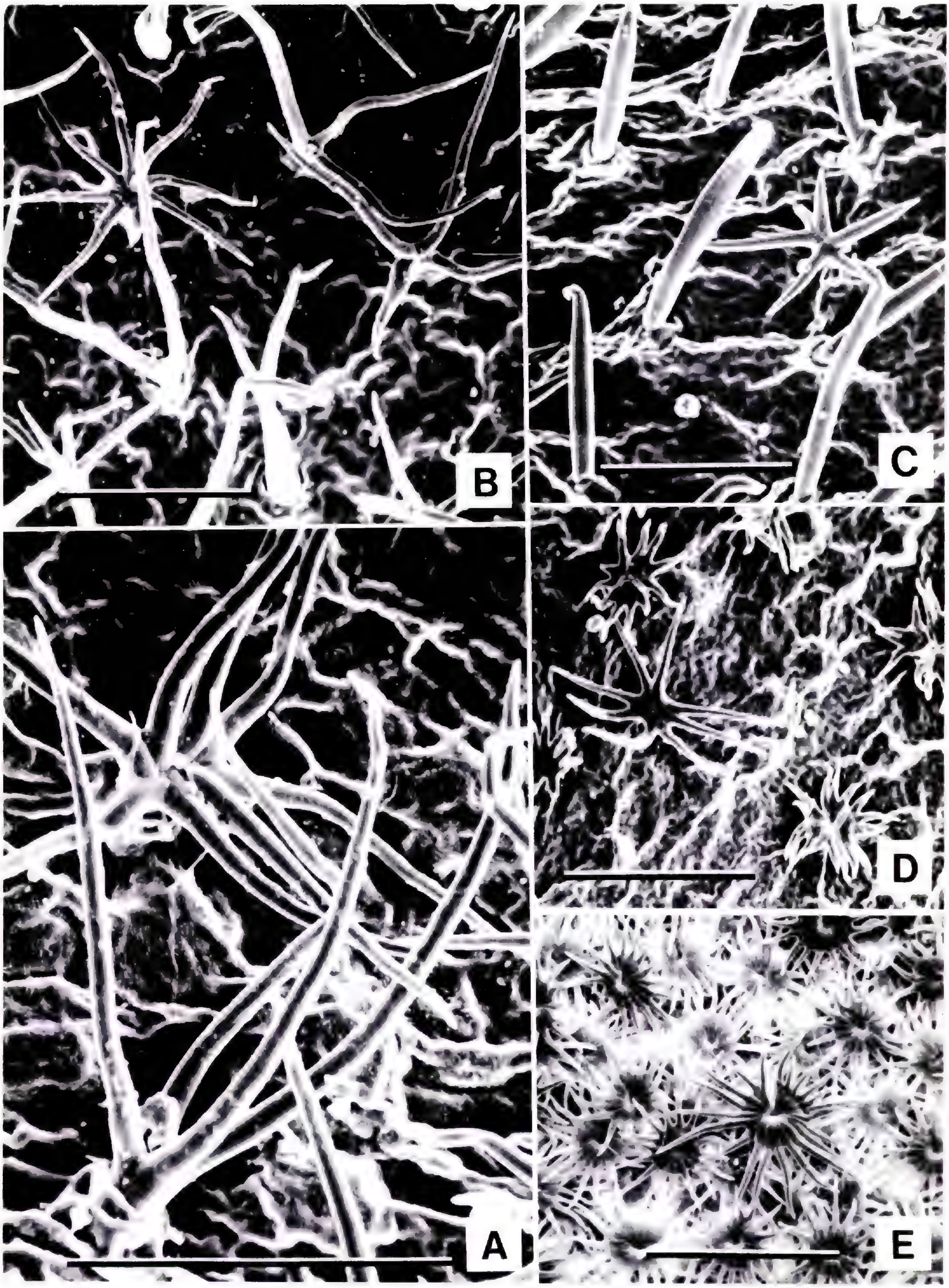


FIGURE 9. Scanning electron micrographs of *Monimia* leaf trichomes.—A. *M. amplexicaulis,* adaxial leaf surface, *Capuron SF-28210* (P).—B. *M. rotundifolia,* adaxial leaf surface, *Friedmann 781* (P).—C. *M. rotundifolia,* adaxial leaf surface, *Bosser 21332* (P).—D. *M. ovalifolia,* adaxial leaf surface, *Guého sub MAU 14097* (MAU).—E. *M. ovalifolia,* abaxial leaf surface, *Friedmann 1884* (P). Bars equal 0.5 mm.

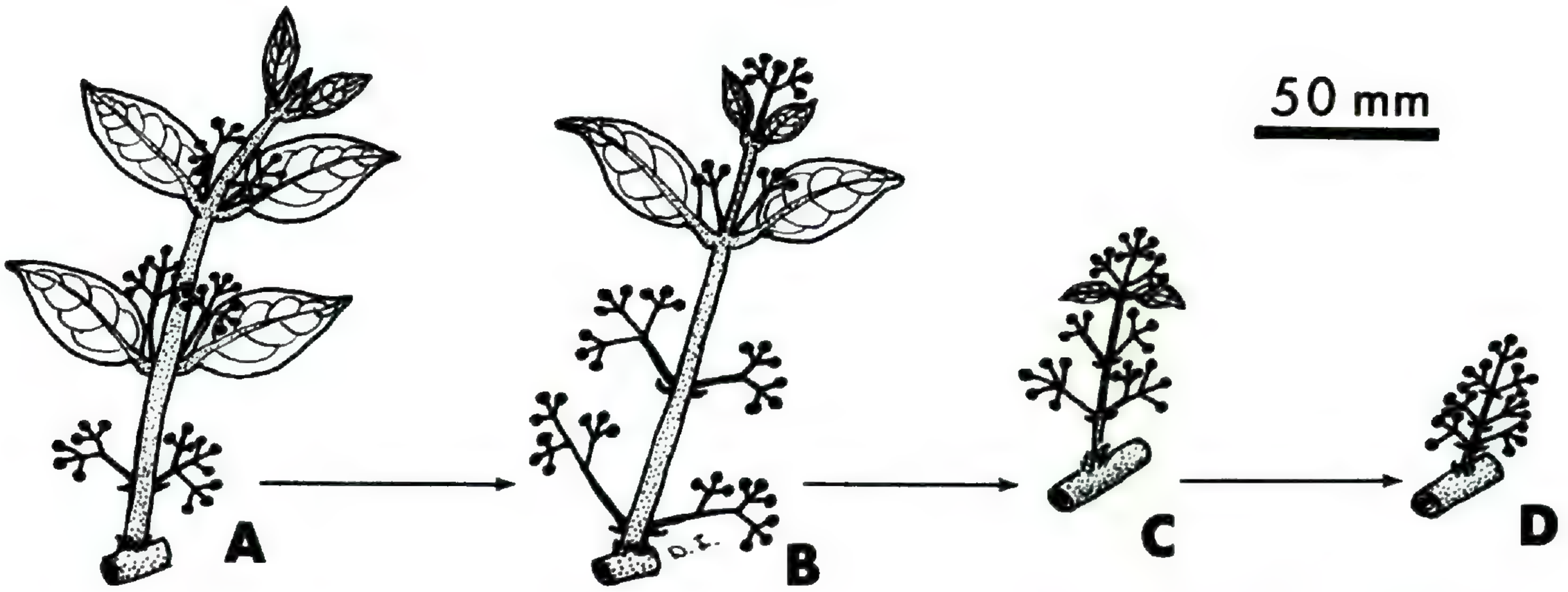


FIGURE 10. *Monimia* inflorescence types, hypothetical reduction series showing derivation of different types. Flowers are depicted as being in one plane, whereas they are actually decussately arranged.—A. Indeterminate leafy shoot with axillary thyrses.—B, C. Determinate leafy thyrses.—D. Thyrse. Bar equals ca. 50 mm.

modally distinct for given species. A brief review of the inflorescence characters will be given for each genus.

Observations on numerous herbarium specimens and living plants reveal that all three species of *Monimia* are dioecious. Inflorescences of all three species are extremely polymorphic and have been variously described as panicles, umbels, racemes (e.g., Baker, 1877), and cymes (Hutchinson, 1964). The ultimate determinate floral unit consists of from two to eight, but usually three, flowers on subequal pedicels attached to a common axis at the same point. As all the flowers in the unit are of the same sex and size, and furthermore all open at about the same time, it does not represent a cyme or pleiochasium in the usual sense (e.g., Lawrence, 1951), but is truly umbelloid. Groups of two to four umbelloid units may be further aggregated or dispersed along a common axis in a thyrse-like manner. The resulting units are borne decussately on a central axis in various ways; up to four different inflorescence types may occur on a given individual, all ramiflorous. These appear to represent a reduction series from an indeterminate leafy shoot with simple axillary thyrses to a leafless, determinate thyrse (Fig. 10A–D).

A) The discrete umbelloid or thyrsic floral units are axillary and occasionally subfoliar on leafless nodes near the basal portion of the actively growing, indeterminate leafy shoot. Each subfoliar unit is subtended by a single caducous, brown bract presumably representing a reduced leaf.

B) The next stage involves the addition of a terminal floral unit. Addition of further lateral units with a concomitant reduction in the number of leaves, which are replaced by bracts, results in the entire structure becoming a determinate leafy thyrse.

C) Further suppression of leaves and shortening of the floral axis results in a more contracted, but still leafy, thyrse.

D) Finally, suppression of all the leaves and their replacement by bracts and still further shortening of the floral axis results in a true thyrse. A similar reduction series occurs in *Tambourissa,* ultimately resulting in a monochasium.

In *Monimia ovalifolia,* the ultimate floral units are generally quite contracted, although the secondary axes may be elongated, with up to 87 flowers per inflorescence. The inflorescence of *M. amplexicaulis* is invariably short and contracted, consisting of not more than 37 flowers in specimens I have examined. Inflorescence structure is much more variable in *M. rotundifolia,* ranging from short and contracted to lax and elongated with up to 76 flowers. Plants of the latter type were described as *M. citrina* by Tulasne. Such variation may occur within a single population, e.g., at Col de Bellevue, Réunion (*Lorence 2471–2474*; *2773–2775,* all MO). In view of the variability of inflorescence structure in *Monimia,* it is not a particularly useful taxonomic character.

The basic inflorescence unit in the three species of *Decarydendron* (all monoecious) is a sexually mixed or unisexual pleiochasium (termed "spiciform" by Danguy, 1928). It consists of an elongated floral axis bearing two to four decussate or subalternate pairs of pedicellate androecious

TABLE 5. Selected gross morphological features of *Tambourissa* species according to Group.

Species	Group	Distr.	Vegetat. Pubesc.	Phyllotaxis	Leaf Marg.	Inflr. Posn.	Inflr. Type	Inflr. Composn.
T. thouvenotii	1A	Mad.	velutin.	opposite	toothed	rami., axil.	pleiochasium, solit.	mixed
T. trichophylla	1A	Mad.	pilose-tomentose	opposite	toothed	rami., axil.	pleiochasium	mixed
T. uapacifolia	1A	Mad.	velutin.	opposite	entire	rami.	pleiochasium	unisex.
T. decaryana	1B	Mad.	pilose-hirsute	opposite	entire	cauli.	pleiochasium	unisex.
T. hildebrandtii	1B	Mad.	villous	opposite	entire	rami., axil.	pleiochasium, solit.	mixed
T. humbertii	1B	Mad.	hirsute	opposite	entire	cauli.	fascic., pleiochasium	unisex.
T. nitida	1B	Mad.	pilose	opposite	entire	axil.	pleiochasium, solit.	mixed
T. nosybensis	1B	Mad.	pilose	opposite	entire	cauli.	pleiochasium	unisex.
T. floricostata	1C	Mad.	subglab.	opposite	entire	rami., axil.	pleiochasium, solit.	unisex.
T. parvifolia	1C	Mad.	subglab.	opposite	entire	rami.	pleiochasium	unisex.
T. beanjadensis	2A	Mad.	glabrous	opposite	entire	rami.	pleiochasium	unisex.
T. comorensis	2A	Gde. Comore	subglab.	opposite	entire	rami., cauli.	pleiochasium	mixed
T. crassa	2A	Réun.	subglab.	opposite	entire	term.	solit.	unisex.
T. elliptica	2A	Réun.	subglab.	opposite	entire	cauli., rami., axil.	fascic., pleiochasium, solit.	mixed (unisex.)
T. leptophylla	2A	May.	finely pubesc.	opposite	entire	cauli., rami., axil.	thryse, pleiochasium, solit.	unisex. (mixed)
T. madagascariensis	2A	Mad.	subglab.	opposite	entire	rami.	pleiochasium	unisex.
T. kirkii	2B	Anj.	hirsute	opposite	entire	?	pleiochasium	unisex. (?)
T. paradoxa	2B	Anj.	glabrous	opposite	entire	rami., axil.	pleiochasium, solit.	unisex.
T. capuronii	3	Mad.	glabrous	opposite	entire	cauli.	pleiochasium	unisex. (mixed)
T. moheliensis	3	Moh.	subglab.	opposite	entire	cauli., rami.	thyrse, pleiochasium	unisex.
T. gracilis	4	Mad.	glabrous	opposite	entire	rami.	pleiochasium	unisex.
T. purpurea	4	Mad.	glabrous	opposite	entire	rami., axil., term.	pleiochasium, dichas., solit.	mixed, unisex.

TABLE 5. Continued.

Species	Group	Distr.	Vegetat. Pubesc.	Phyllotaxis	Leaf Marg.	Inflr. Posn.	Inflr. Type	Inflr. Composn.
T. religiosa	4	Mad.	glabrous	opposite	entire	rami., axil., term.	pleiochasium, dichas., solit.	mixed, unisex.
T. amplifolia	5	Maur.	subglab.	opposite	entire	cauli. (rami.)	pleiochasium, fascic, solit.	mixed, unisex.
T. cocottensis	5	Maur.	glabrous	opposite	entire	cauli.	fascic., solit.	unisex.
T. cordifolia	5	Maur.	glabrous	opposite	entire	rami., cauli.	solit., fascic.	unisex.
T. pedicellata	5	Maur.	subglab.	opposite	entire	rami., cauli.	pleiochasium, dichas.	unisex. (mixed)
T. tau	5	Maur.	subglab.	opposite (in pseudoverticels)	entire	cauli., rami., axil.	dichas., fascic., solit.	unisex., mixed
T. tetragona	5	Maur.	glabrous	opposite	entire	cauli.	pleiochasium	unisex.
T. bathiei	6	Mad.	hirsute	opposite	entire	cauli.	pleiochasium, thyrse	unisex.
T. sieberi	6	Maur.	velutin.-toment.	opposite	entire	cauli.	thyrse, pleiochasium	unisex.
T. perrieri	7	Mad.	subglab.	opposite	entire	cauli.	pleiochasium	unisex., mixed
T. quadrifida	7	Maur.	glabrous	opposite	entire	cauli. (rami.)	thyrse, pleiochasium	unisex. (mixed)
T. alaticarpa	8	Mad.	villous	opposite	toothed	cauli.	pleiochasium	mixed (unisex.)
T. longicarpa	8	Mad.	velutin.	opposite	toothed	cauli.	pleiochasium	mixed (unisex.)
T. castri-delphinii	9	Mad.	glabrous	ternate	entire	rami.	pleiochasium, fascic.	unisex.
T. ficus	9	Maur.	pilose-tomentose	ternate	entire	cauli.	solit., fascic.	unisex. (mixed)
T. peltata	9	Maur.	glabrous	ternate	entire	rami. (cauli.)	solit., fascic.	unisex.

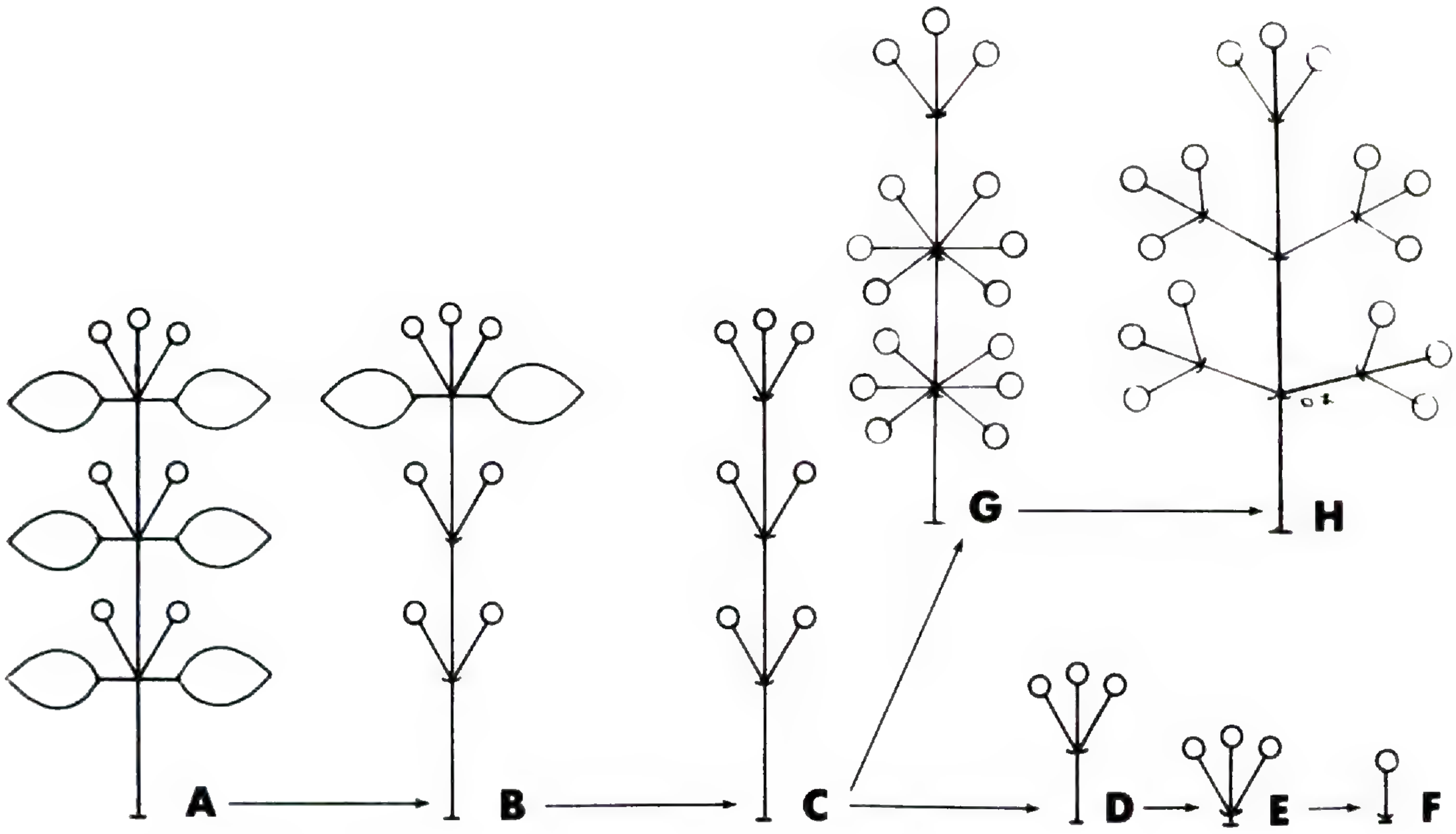


FIGURE 11. Schematic diagrams of *Tambourissa* inflorescence types showing hypothetical reduction (A–F) and elaboration (C, G, H) series.—A, B. Leafy pleiochasia.—C. Pleiochasium.—D, E. Dichasia.—F. Monochasium.—G. Pleiochasium.—H. Thyrse. Flowers are depicted as being in one plane, whereas they are actually decussately arranged. Not to scale.

flowers terminated by a single gynoecious or androecious flower. In all three species the floral axis and pedicels are velutinous or puberulent and the pedicels are generally minutely bracteolate (Fig. 14E). The inflorescence is usually basally cauliflorous in *D. perrieri,* and cauli- or ramiflorous in *D. lamii* and probably also in *D. helenae.*

In *Ephippiandra* (all monoecious), the inflorescence is a sparsely to densely pubescent dichasium or fascicle, or the flowers may be solitary. In *E. capuronii, E. domatiata, E. madagascariensis,* and *E. tsaratanensis* it is an axillary three- or five-flowered sexually mixed dichasium produced on the new growth (Fig. 14F, G). The terminal, central gynoecious flower appears to mature first in the dichasium, after which the lateral androecious flowers come into anthesis. In *E. myrtoidea,* the androecious flowers are axillary, either solitary or in three-flowered fascicles or dichasia, whereas the gynoecious flower is terminal, either solitary or in a three- or five-flowered dichasium with lateral androecious flowers. A similar pattern occurs in *E. microphylla,* although the flowers are solitary with the androecious flowers being axillary and the gynoecious flowers terminal on the stems. In all the species, the short to long floral pedicels are subtended by a pair of acute bracteoles and the peduncles may also be bracteolate.

Tambourissa displays a diverse array of inflorescence types, ranging from elaborate multiflowered thyrses on the one hand to extremely reduced, single-flowered monochasia on the other (Table 5). Pubescence of the floral axes and pedicels varies greatly, from totally glabrous to densely velutinous-tomentose. In all species the pedicel is subtended by one or rarely several minute bracteoles, and the floral axis also bears several pairs of decussate bracteoles basally. Pedicel length is relatively constant for a given species.

A short, determinate pleiochasium is the most widespread inflorescence type in the genus, occurring occasionally or consistently in 32 of the 43 species. This inflorescence type consists of a number of decussately arranged floral pairs spaced along a short to elongated floral axis (Fig. 11C). Although pleiochasia of this type are unisexual in many species (e.g., *T. tetragona*), in others the flowers may be randomly mixed sexually (e.g., *T. pedicellata*), and in yet others they are frequently terminated by a single gynoecious flower with lateral androecious flowers (e.g., *T. hildebrandtii, T. longicarpa*). In this case the flowers of one sex (usually gynoecious) generally open first and it is therefore a cyme in the classical

sense (e.g., Lawrence, 1951). The pleiochasia may be axillary, ramiflorous, or rarely cauliflorous.

The pleiochasial inflorescence may be derived from a leafy stem with solitary, axillary, and terminal flowers by gradual reduction of the leaves into bracteoles, and by a concomitant shortening of the main axis (Fig. 11A–C) similar to that described for *Monimia*. Single individuals of species such as *T. elliptica* (*Lorence 2528*, MO) and *T. pedicellata* (*Lorence 2584–2586*, all MO) often show the entire range of stages in the reduction series. As *Tambourissa pedicellata* is one of the least specialized species in terms of floral morphology, it may have possibly retained an unspecialized inflorescence type as well. Gottsberger (1974) considers lateral flowers or few-flowered inflorescences to be unspecialized in primitive angiosperms, from which other types have been derived.

Further shortening and reduction of the pleiochasium ultimately results in a dichasium of three flowers supported by a short peduncle (Fig. 11D, E), which may either be ramiflorous as in *Tambourissa castri-delphinii*, a dioecious species, or terminal and axillary as in *T. purpurea* and *T. religiosa*, which have sexually mixed dichasia or pleiochasia. Suppression of both lateral flowers thus results in a single-flowered monochasium (Fig. 11F), as in *T. ficus* or *T. tau*, which are cauli- and ramiflorous respectively, and in *T. crassa*, which has terminal flowers. Many of the cauliflorous species are subdioecious or dioecious and produce clusters or fascicles of monochasia from knobby meristematic swellings on the trunk. That the pedicel is jointed to a distinct peduncle, where it often bears one of more pairs of decussate bracteoles, suggests that it is a reduced inflorescence and not merely a solitary flower per se. Ontogenetic studies are required to confirm this, however.

At the opposite extreme, a number of species have compound inflorescences with numerous flowers that may be derived by an elaboration of the pleiochasium. In species such as *Tambourissa quadrifida* (Group 7), there has been a multiplication of the floral pairs into cymose or umbelloid units of three to five flowers (Figs. 11G, 20B).

The two species in Group 8 (*T. alaticarpa* and *T. longicarpa*) also possess pleiochasia with the androecious flowers produced in lateral umbelloid or cymose groups of one to three, whereas one to three gynoecious flowers are segregated in a terminal unit (Fig. 17A). The terms cymose and umbelloid are used loosely here, as the flowers of a group may either mature simultaneously or in a staggered, random fashion. Pleiochasia with terminal gynoecious and lateral androecious flowers also occur in *T. perrieri* (Group 7) and *T. hildebrandtii* (Group 1B).

Floral units in other species such as *T. sieberi* and *T. bathiei* (Group 6) are produced on distinct peduncles and the resulting inflorescence is thyrsic (Fig. 11H). In these species, the inflorescences tend to be cauliflorous and predominantly unisexual, although flowers of the opposite sex are occasionally intermixed.

In summary, although inflorescence type and position may vary considerably in the four genera discussed above, they are frequently modally distinct for given species and often provide a number of taxonomically important features.

FLORAL MORPHOLOGY AND ANATOMY

In terms of floral morphology, the Monimiaceae are an extremely diverse, and at the same time, coherent family in which many of the genera exhibit trends towards floral specialization, often via reduction (Perkins & Gilg, 1901; Perkins, 1911, 1925; Money et al., 1950). The following general evolutionary trends in the Monimiaceae sensu lato have been summarized by Corner (1976) and Endress (1980b):

1) Transition from floral bisexuality to unisexuality.
2) Reduction in size and number of parts.
3) Transition from spiral, to radial, to decussate arrangement of parts.
4) Massive development of the receptacle (floral cup) which assumes the functions of a perianth and ovary wall.
5) Closure of the receptacle, involving:
   A) Enclosure of the inner tepals by the receptacle.
   B) Enclosure of the carpels (ovaries) by the female receptacle.
   C) Permanent closure of the gynoecious receptacle, which dehisces only in fruit.
   D) Enclosure of the stamens by the androecious receptacle, which splits open flat by lateral fissures at anthesis, or remains partly closed.
6) Transition from free, stalked, or sessile carpels borne on the flattened or shallow receptacle, to inferior syncarpous carpels immersed in the receptacle wall.

7) Production of a mucilaginous compitum, and finally a "hyperstigma" which assumes a stylar function.
8) Apical (or rarely basal) fusion of the anther loculi into a single loculus with a progressive shortening and broadening of the filament.

Although many of these trends are most apparent at the subfamilial or tribal levels (see discussion under Taxonomic History of the Monimiaceae), a significant number also occur within the Mollinedioideae (sensu Thorne) and occasionally within a single genus (e.g., *Tambourissa*). The four genera belonging to the two subfamilies discussed here are all relatively specialized, i.e., have unisexual flowers lacking an elaborate petaloid perianth. Although *Monimia* displays a number of the same features as the other three genera, it will be discussed first as it belongs to a separate subfamily, the Monimioideae. Because the other three genera, all Mollinedioideae, display obvious trends involving three levels of specialization and form a natural coherent series, they will be discussed as such.

Floral construction in *Monimia* is reduced, highly specialized, and very similar in all three species. Flowers of both sexes have closed, globular receptacles in bud surmounted by three to six minute, decussate, scale-like tepals (Perkins & Gilg, 1901; Money et al., 1950). In *Monimia,* the receptacle has assumed the function of the perianth and in the gynoecious flowers turns orange or red at anthesis. The globose, internally pubescent gynoecious receptacle encloses several free, subsessile carpels, each with a single pendulous, anatropous ovule. At anthesis, the receptacle opens by means of a small, three to six lobed apical pore through which the glistening, slightly papillose white styles are exserted (Figs. 12.1A, 14B).

At anthesis, the androecious flower splits open by lateral fissures into four to six valvate, ultimately recurved lobes with numerous (ca. 25–150) irregularly disposed, white bisporangiate stamens. Each stamen bears a pair of white, earlike appendages at or near its base (Fig. 12.1C, D). Anther dehiscence is lateral along the inner, adaxial margins of the monosporangiate loculi, which then open outward like flaps (Figs. 12.1D, 13A) releasing the slightly coalescent pollen. Staminal dehiscence in *Monimia* has been described as subintrorse by Hutchinson (1964), but is more nearly introrse (De Candolle, 1868; Perkins & Gilg, 1901). Observations on living flowers of all three species revealed no apparent nectar production by the stamens as in some Atherospermoideae (Sampson, 1969a), although sweet odors are emitted by flowers of both sexes.

Obvious floral morphological differences in the species are expressed in terms of receptacle size (smallest in *Monimia ovalifolia*), number of stamens (fewest in *M. ovalifolia,* most numerous in *M. amplexicaulis*), and in stamen length (shortest in *M. ovalifolia,* longest in *M. rotundifolia*). Flowers of both sexes are externally pubescent, and trichomes furnish additional useful specific characters. A more detailed study of the ontogeny and floral construction in *Monimia* is forthcoming (Endress & Lorence, in prep.).

The three genera belonging to the Mollinedioideae form a natural series in which three evolutionary levels of floral morphological specialization are obvious, primarily in the gynoecious flowers. The least specialized genus is *Decarydendron,* and the most specialized is *Tambourissa* (Fig. 12.2–12.4).

1) *Decarydendron:* receptacles of both sexes are shallowly cupuliform and open gradually without splitting at anthesis; tepals are large, numerous, in radial series; carpels are free, numerous, long and clavate, subsessile; fruiting carpels are presumably exposed (?); stamens have a distinct filament and separate loculi (Fig. 12.2A–D).

2) *Ephippiandra* (including *Hedycaryopsis*): gynoecious receptacles are discoid and develop gradually without splitting at anthesis; tepals are few, small, decussate; carpels are free, fewer and shorter, columnar, sessile; fruiting carpels are basally immersed in the receptacle; androecious receptacle is closed in bud, splitting open by longitudinal fissures at anthesis; stamens are subsessile, with short, broad filaments, loculi are free or confluent (Fig. 12.3A–D).

3) *Tambourissa* (including *Phanerogonocarpus*): gynoecious receptacle is closed, globular to cylindrical, the apex often splitting partly open at anthesis; tepals are few, minute, decussate; carpels are inferior, syncarpous; fruiting carpels are enclosed; fruiting receptacle splits open at maturity; androecious receptacle is closed in bud, splitting open by longitudinal fissures at anthesis; stamens have distinct filaments or are short and sessile, loculi are free or confluent (Fig. 12.4A–D).

Both androecious and gynoecious flowers of *Decarydendron* are relatively monomorphic, somewhat subglobose in bud, and have seven to 15 large, thick, obtuse tepals in two or three

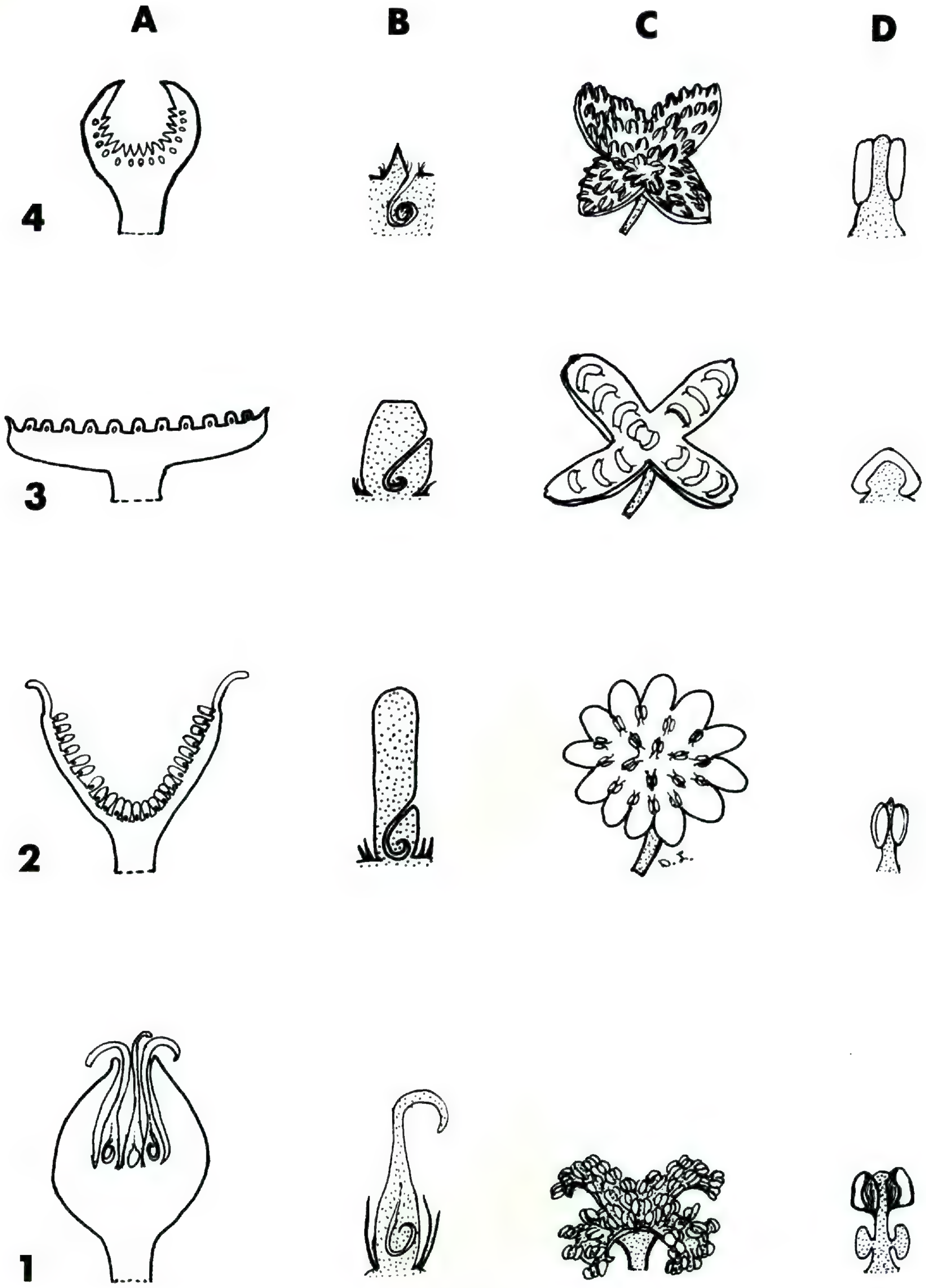
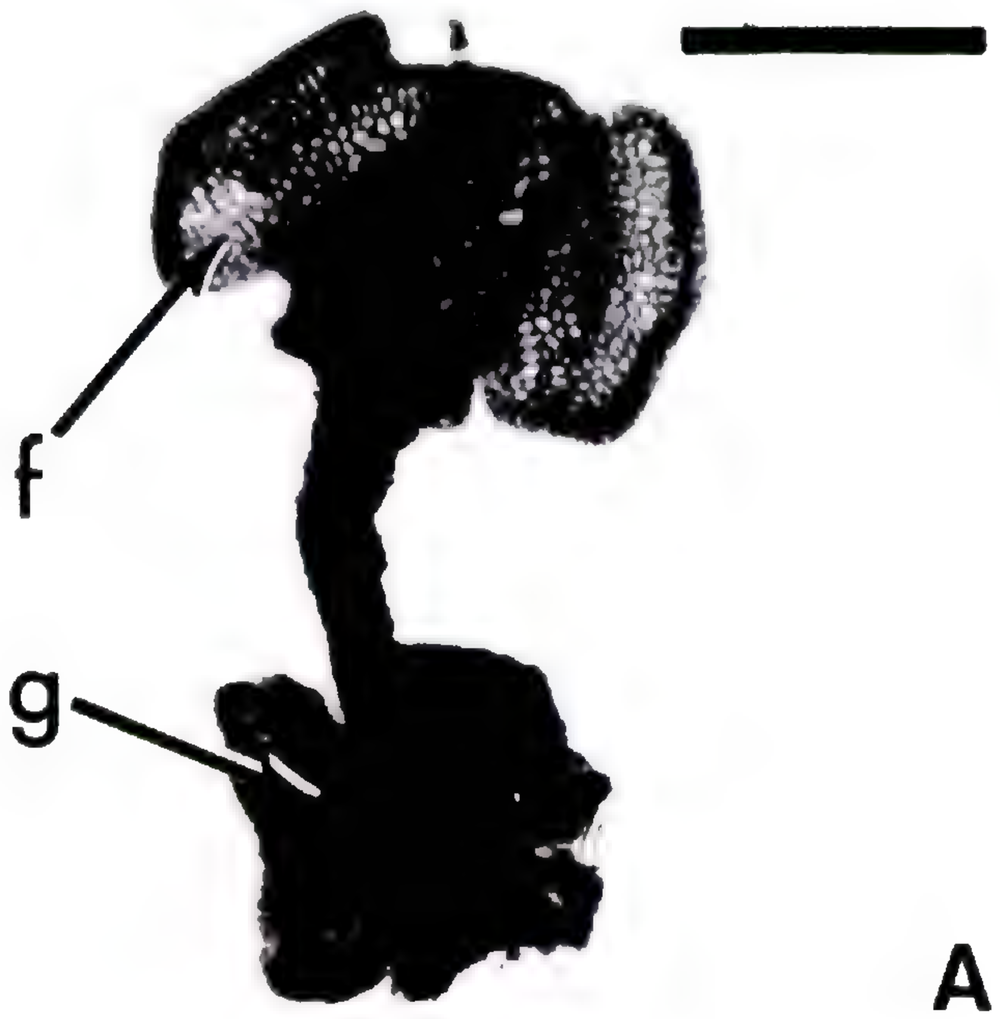


FIGURE 12. Schematic drawings of flowers of the four genera of Monimiaceae in the Malagasy region. 1. *Monimia*; 2. *Decarydendron*; 3. *Ephippiandra*; 4. *Tambourissa*.—A. Gynoecious flower, longitudinal section.—B. Individual carpel, longitudinal section.—C. Androecious flower at anthesis.—D. Stamen. Not to scale.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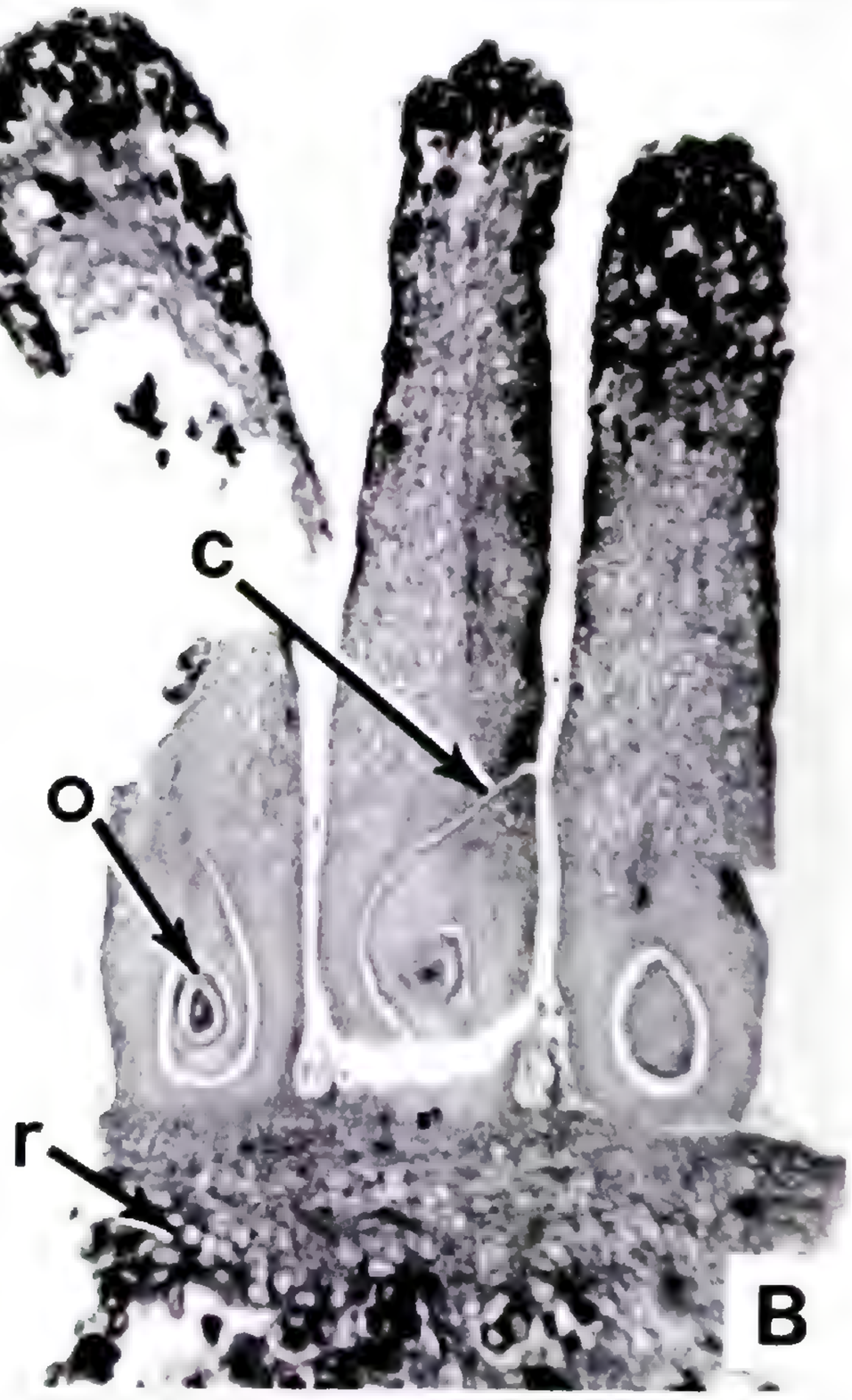
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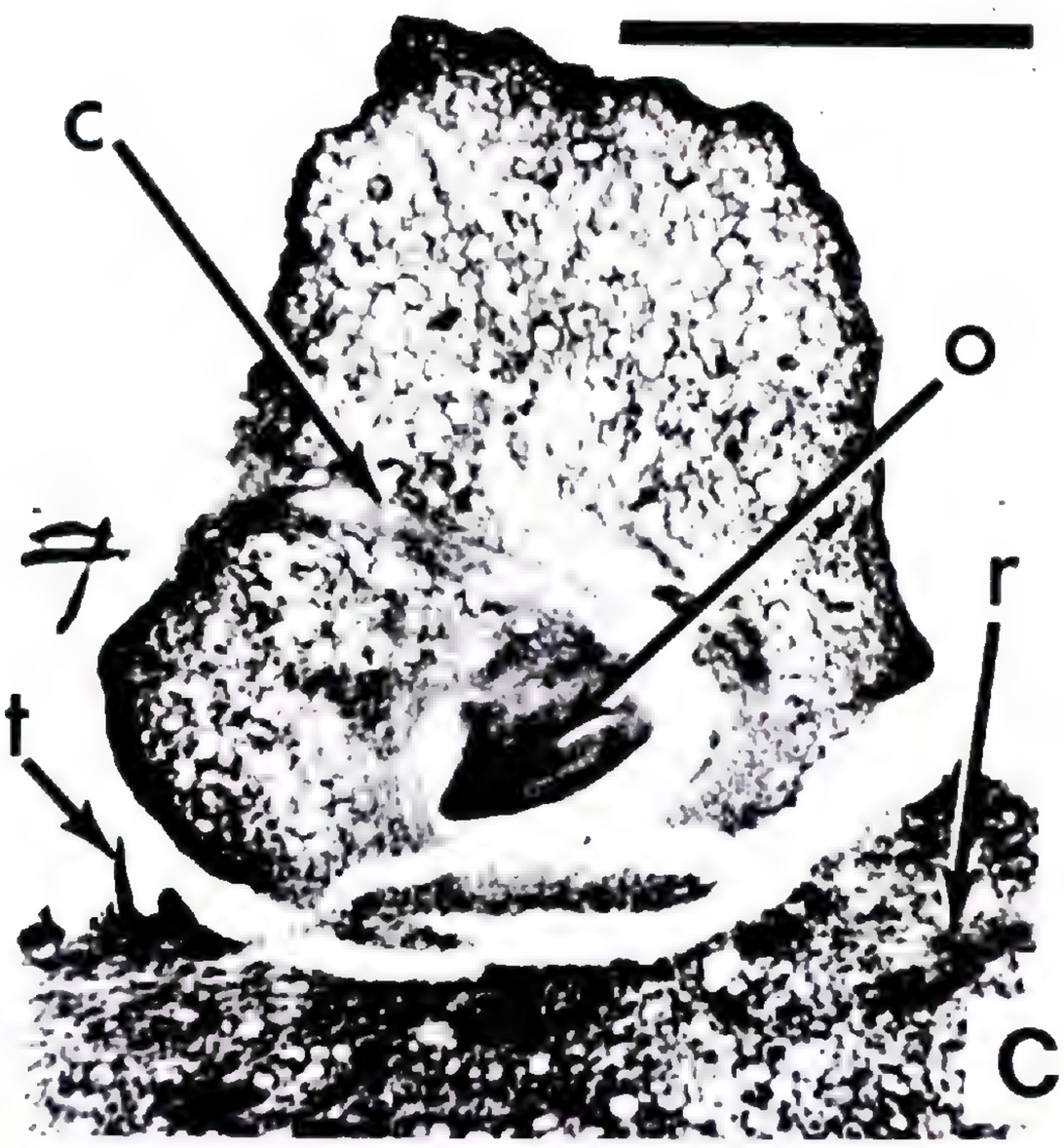
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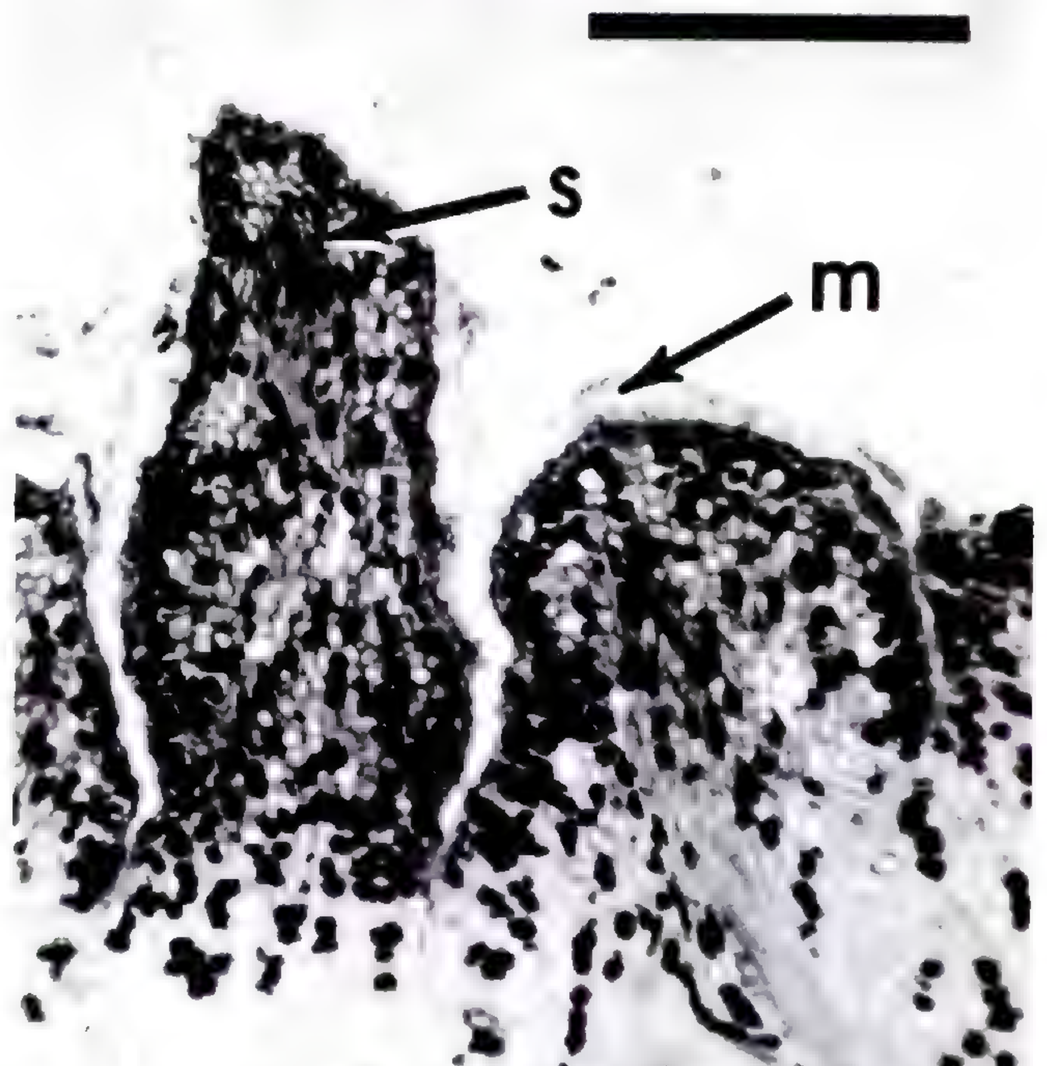
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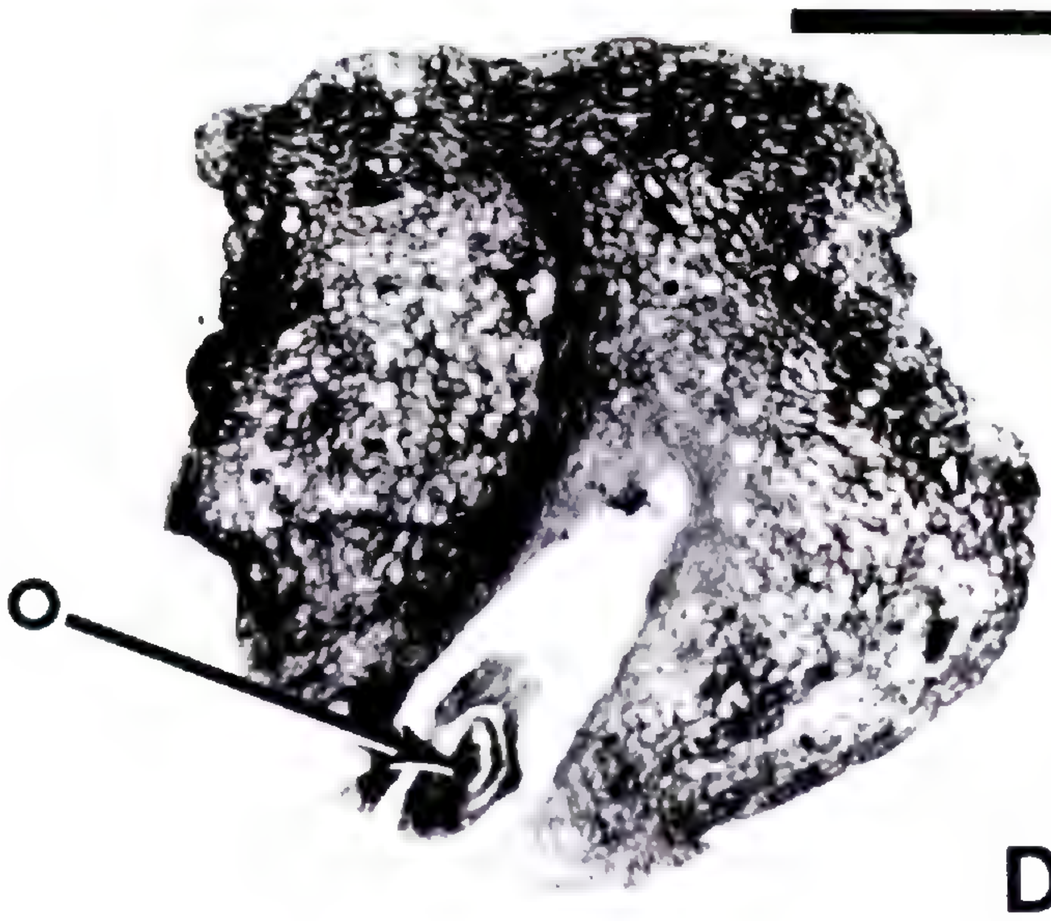
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whorled series. The tepals are infolded in bud and the flowers consequently do not split, but open gradually at anthesis as the tepals become erect or everted. The external receptacle surface is often pubescent with simple trichomes.

At anthesis the gynoecious flower of *Decarydendron* is hemispherical or obconical with thick walls and straight or slightly incurved tepals. Numerous free, clavate carpels line the inner receptacle surface (ca. 300 in *D. helenae*) and are interspersed with short, densely tufted simple lignified trichomes. In *D. helenae* var. *stenophyllum* (*Humbert 6613,* K), each carpel is clavate or cylindrical, ca. 1.5 mm long, slightly constricted basally and obtuse apically (Fig. 13B). A single, pendulous anatropous bitegmic ovule is contained in a small loculus which is confined to the base of the carpel and from which the oblique stylar canal runs upward and opens at the side of the carpel in its basal third (Fig. 13B). The carpellary ground tissue contains scattered oil cells above the ovary and densely aggregated stone cells in the terminal portion (Fig. 13B). Stone cells also occur in the receptacular ground tissue, but no tanniferous idioblasts were observed. In cleared carpels, a single vascular bundle enters from the base, supplies the ovule, and extends upward almost to the apex, terminating in tracheoids. The exterior surface of the carpel is possibly secretory in nature as in many Monimiaceae (Endress, 1980b), but no traces of mucilage were observed.

In the androecious flower, from 16 to 60 stamens are irregularly dispersed over the glabrous to pubescent inner surface of the shallowly concave or cupuliform receptacle (Figs. 12.2C, 14E). Stamens of all three species are comparatively unspecialized with a distinct, narrow filament, unprolonged connective, and separate, laterally dehiscent, tetrasporangiate anthers (Fig. 12.2D).

Useful taxonomic features of *Decarydendron* flowers include: number and size of tepals and characters of their margins (crenulate or not); number of stamens; size of the receptacle and presence or absence of lateral ridges (Cavaco, 1959). The genus is clearly the least specialized florally of the Mollinedioideae in the Malagasy region.

Floral construction in *Ephippiandra* (including *Hedycaryopsis*) is more specialized, including a strong male/female floral dimorphism (Figs. 12.3A–D, 14F, G). Gynoecious flowers are somewhat globular and concave in bud, but open gradually and become discoid during ontogenetic development. In *Ephippiandra madagascariensis* (*Bernardi 11977,* K, MO), the receptacular rim initially bears four small, decussate, deltoid tepals which apparently divide once by lateral doubling, resulting in eight tepals in the mature flower. Most species also appear to have four, eight, or rarely 16 minute, decussate tepals, and the receptacles are externally pubescent with short to long simple hairs. At anthesis the receptacle is flat and discoid, crowded with 20–150 free, sessile, shortly columnar carpels interspersed with clusters of simple, lignified trichomes (Fig. 12.3A, B). Each carpel is four to six sided, ca. 1–1.5 mm long, with a flat top, straight to inclined sides, and a slightly constricted base (Fig. 13C, D). The solitary ovule is anatropous or amphitropous and bitegmic, situated in a small loculus near the base of the carpel, with a stylar canal leading obliquely upward and opening at the side near the middle of the carpel (Fig. 13C, D). The entire carpel is covered by an epidermal layer which appears to be secretory and produce mucilage at least around a central zone. Occasional short, simple hairs occur on the carpellary surface in *E. madagascariensis.* In cleared carpels, two vascular bundles enter from the base on either side of the ovule in *E. myrtoidea, E. madagascariensis,* and *E. tsaratanensis,* and fan out into a zone with numerous, terminal tracheoids near the apex. Endress (1980a) also found tracheoids in other genera and suggested that they might function as water storage cells. The ventral bundle gives rise to a weak, arcuate secondary branch supplying the ovule. The floral ground tissue of *E. myrtoidea* contains oil cells, stone cells, and large numbers of tanniferous idioblasts. That of *E.*

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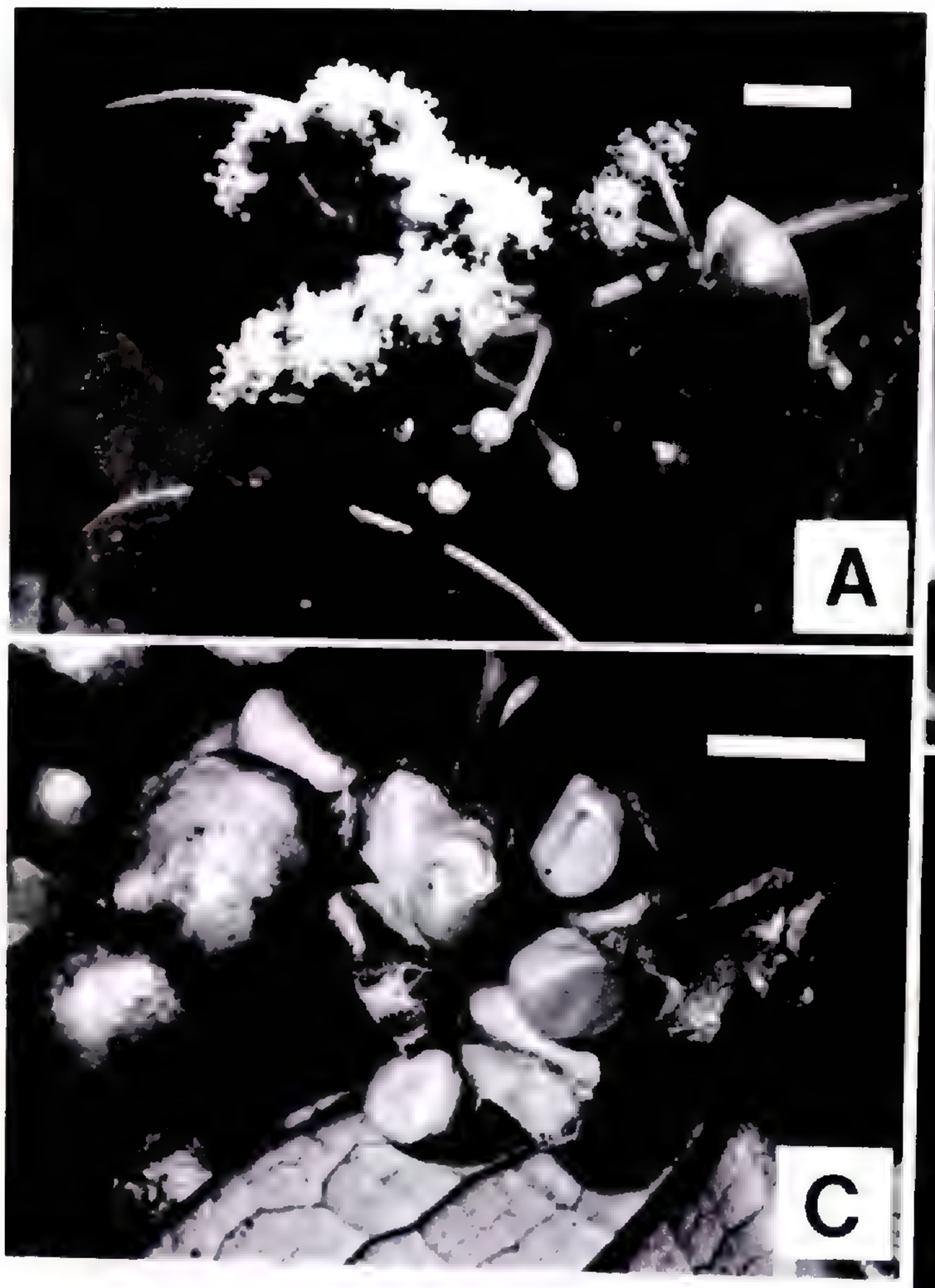
FIGURE 13. Photomicrographs of floral parts.—A. Stamen of *Monimia amplexicaulis* showing nearly introrse dehiscence and basal glands, whole mount, *Lorence 2444* (MO).—B. Carpels of *Decarydendron helenae* var. *stenophyllum,* longitudinal section, *Humbert 6613* (K).—C. Carpel of *Ephippiandra madagascariensis,* longitudinal section, *Bernardi 11977* (MO).—D. Carpel of *E. myrtoidea,* longitudinal section, *Parker s.n.* (K).—E. Carpel of *Tambourissa cordifolia,* longitudinal section, *Lorence 2630* (MO). Bars equal 0.5 mm. c = canal leading to ovule; f = flap of anther loculus; g = glands at base of stamen; m = mucilaginous exudate; o = ovule; r = receptacular ground tissue; s = style; t = trichome.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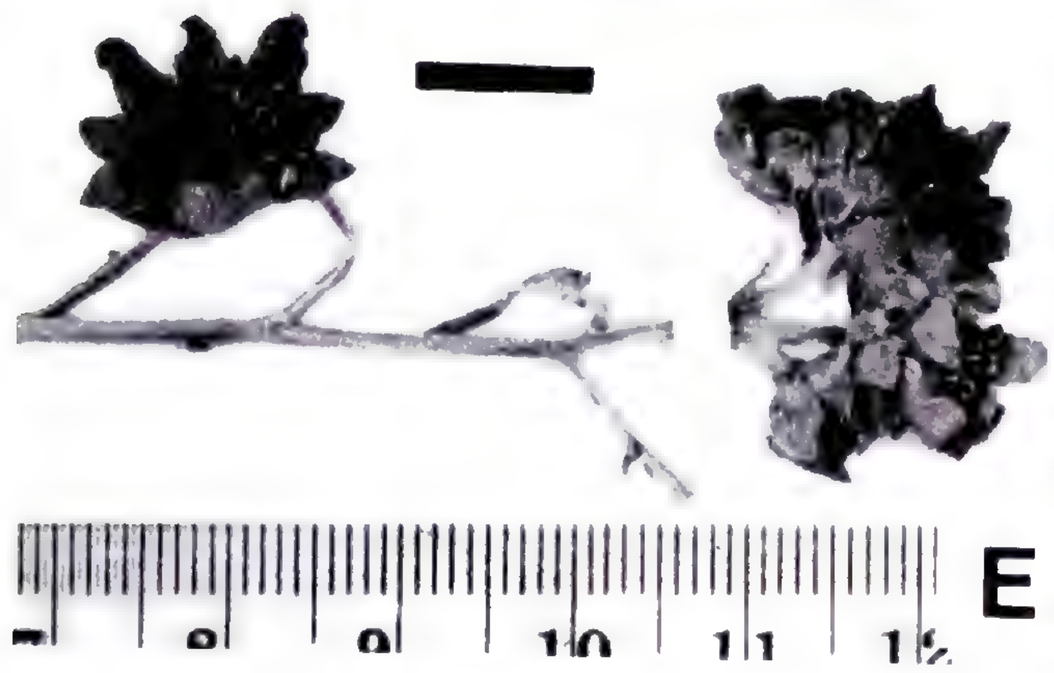
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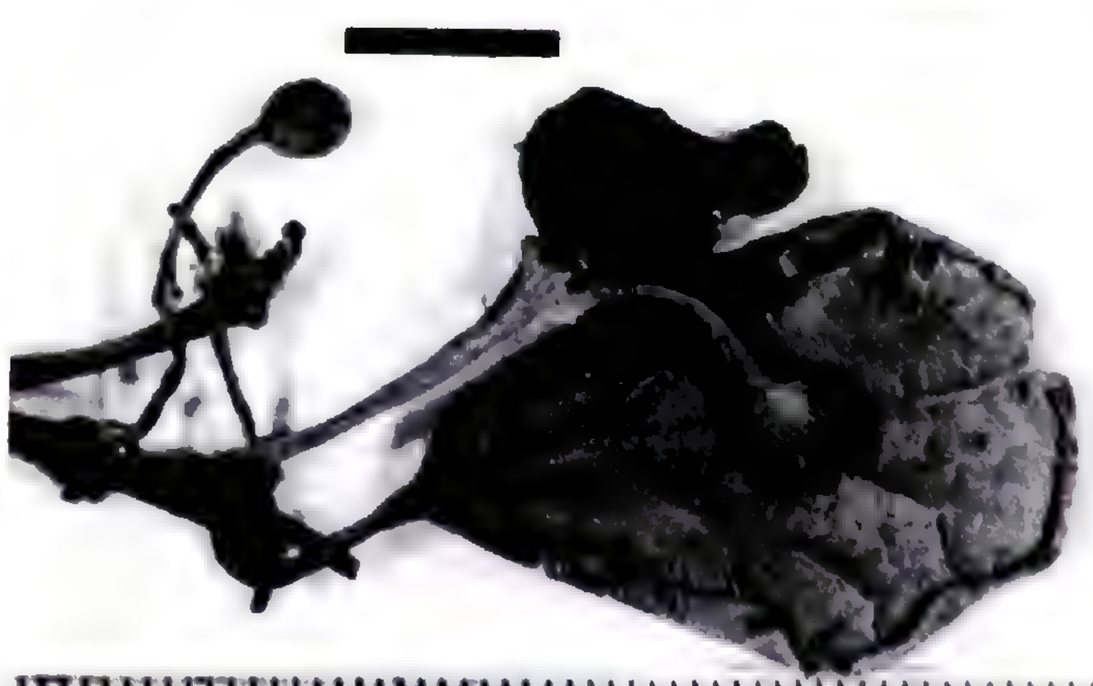
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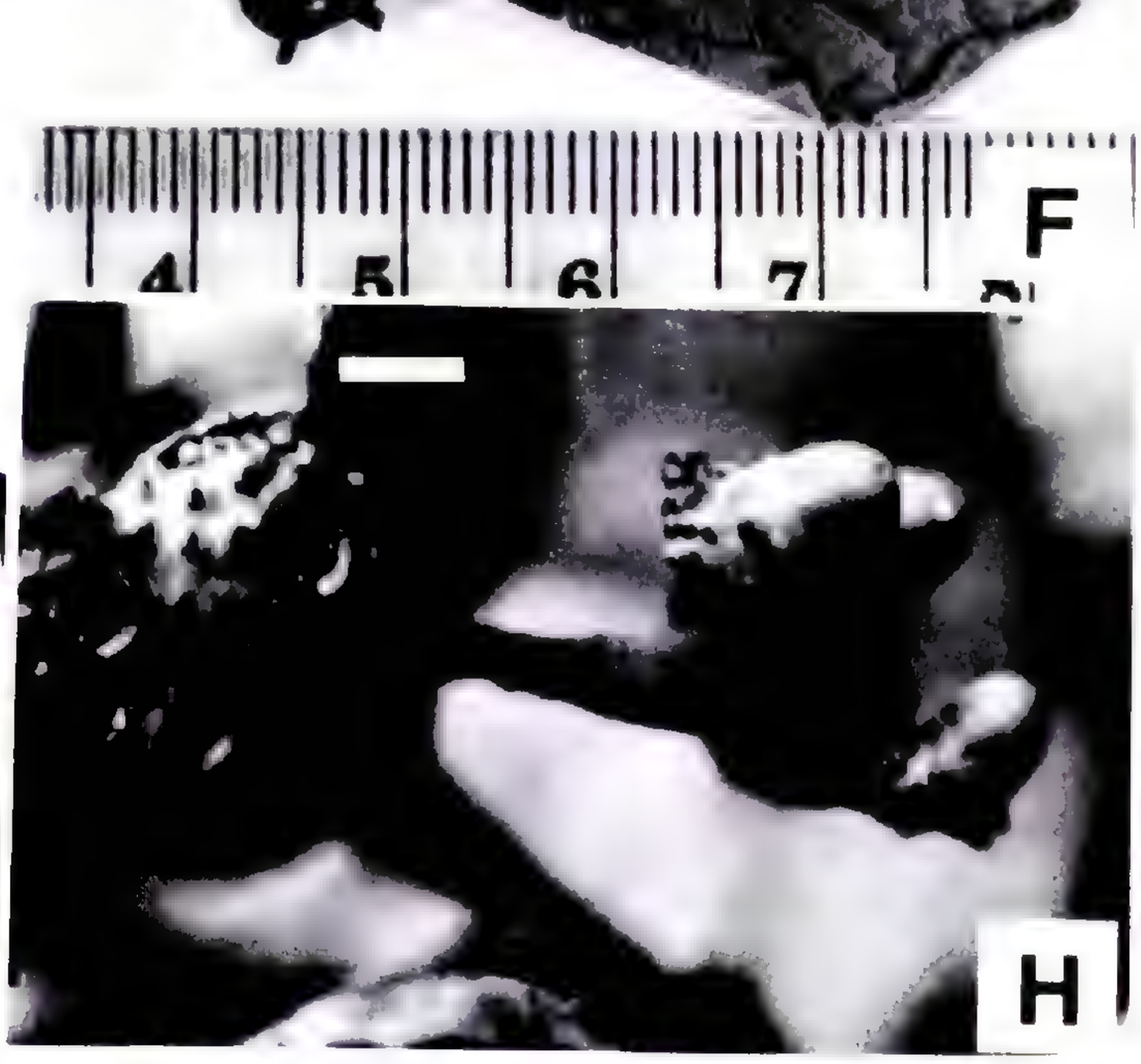
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tsaratanensis contains both oil cells and numerous tanniferous cells, whereas only oil cells occur in *E. madagascariensis*. Receptacular ground tissue of these three species contains idioblasts comparable to those found in the carpels. The fewer and shorter, sessile carpels and reduced, decussate tepals of *Ephippiandra* represent specializations in comparison with *Decarydendron*.

Androecious flowers of *Ephippiandra* are globular and closed in bud (Fig. 14F, G), externally pubescent with short to long simple hairs, and generally bear four pairs of small to minute, acute to deltoid, decussate tepals at or near the apex (Fig. 12.3C, D). At anthesis, the floral cup splits by lateral fissures into four subequal, valvate segments exposing the 9–50 stamens (Fig. 12.3C, D) scattered or situated in several series on the glabrous to pubescent inner receptacle surface. The apex of each lobe usually bears one or rarely two obtuse, scale-like tepals in all but *E. myrtoidea*. The tetrasporangiate stamens range from ligulate and incurved to short, broad, and obtusely deltoid. Those of *E. domatiata, E. madagascariensis, E. perrieri,* and *E. tsaratanensis* are somewhat longer with more distinct filaments, separate loculi, and slightly prolonged or apiculate connectives, whereas those of *E. microphylla* and *E. myrtoidea* are generally shorter and sessile or subsessile with the loculi apically connivent or confluent into a single, crescentiform loculus. Staminal types within the genus intergrade, however, and a comparable range of variation occurs in *Tambourissa*. Dehiscence is lateral and longitudinal, but is continuous in stamens with a single, crescentiform loculus (both separate and confluent loculi may occur in a single flower, e.g., *E. myrtoidea*). *Ephippiandra microphylla* and *E. myrtoidea* have few (10–18), highly reduced stamens with connivent or confluent loculi; these represent specialized features.

Taxonomically useful characters in *Ephippiandra* flowers include: size of the receptacle; number of carpels, stamens, or tepals; presence or absence of tepals on the inner receptacle lobes; size and shape of tepals; size and shape of stamens; condition of the loculi (free or confluent). Floral reduction in the genus shows specialization over *Decarydendron*.

Floral construction in *Tambourissa* (including *Phanerogonocarpus*) displays a number of still more specialized trends, one being a strong androecious/gynoecious floral dimorphism (Fig. 12.4A–D), except in *T. pedicellata, T. purpurea,* and a few other species. Perhaps the most striking and important trend is apparent in the gynoecious flowers, which have their carpels immersed in and fused with the receptacular wall and are therefore inferior and syncarpous (Endress, 1979, 1980b), thus showing considerable advancement over *Decarydendron* and *Ephippiandra*. Although androecious flowers of some *Tambourissa* species are comparable to those of *Ephippiandra,* those of other species are even more specialized. Because a more detailed study of the ontogeny and floral construction of *Tambourissa* has been published elsewhere (Endress & Lorence, 1983), only a brief account is given here.

Gynoecious flowers of *Tambourissa* consist of a massively developed receptacle which is generally closed in bud. Considerable variation occurs in receptacle size and morphology, the main types of which are shown in Figure 15. The receptacle is more or less napiform or cup-like in the majority of species (e.g., *T. cordifolia, T. ficus, T. pedicellata*; Fig. 15B, C, J), but ranges from flat and discoid in *T. peltata* (Fig. 15A), to closed and spherical in *T. sieberi,* or even cylindrical in *T. alaticarpa* and *T. longicarpa* (Fig. 15E, H). Both the flat, open and the closed, globose or cylindrical types appear to be highly specialized and derived from a more generalized cupuliform type like that found in *T. pedicellata*. The receptacles of *T. alaticarpa* and *T. longicarpa,* although extremely elongated and laterally winged, still fall within the range of variation displayed by certain other species. For example,

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FIGURE 14. Flowers and fruits.—A. *Monimia ovalifolia,* androecious inflorescence at anthesis, *Lorence 2896* (MO).—B. *M. ovalifolia,* gynoecious inflorescence at anthesis, note exserted styles (s), *Lorence 2757* (MO).—C. *M. ovalifolia,* ripe fruiting receptacles splitting to expose carpels, *Coode 4954* (K).—D. As for C, *Lorence 2350* (MO).—E. *Decarydendron lamii,* terminal portion of androecious inflorescence with expanded androecious flower showing stamens and large tepals, *Lam & Meeuse 5835* (P).—F. *Ephippiandra madagascariensis,* inflorescences showing globose androecious flowers in bud and central discoid gynoecious flower, *Ursch 66* (P).—G. *E. perrieri,* flowering stem showing globose androecious flowers in bud and discoid central gynoecious flower, *Perrier de la Bâthie 16249* (P).—H. *E. tsaratanensis,* old infructescence with carpels gone (left), and submature infructescence with three green carpels seated in basal cupules (right), *Gentry 11605* (MO). Bars equal 10 mm.

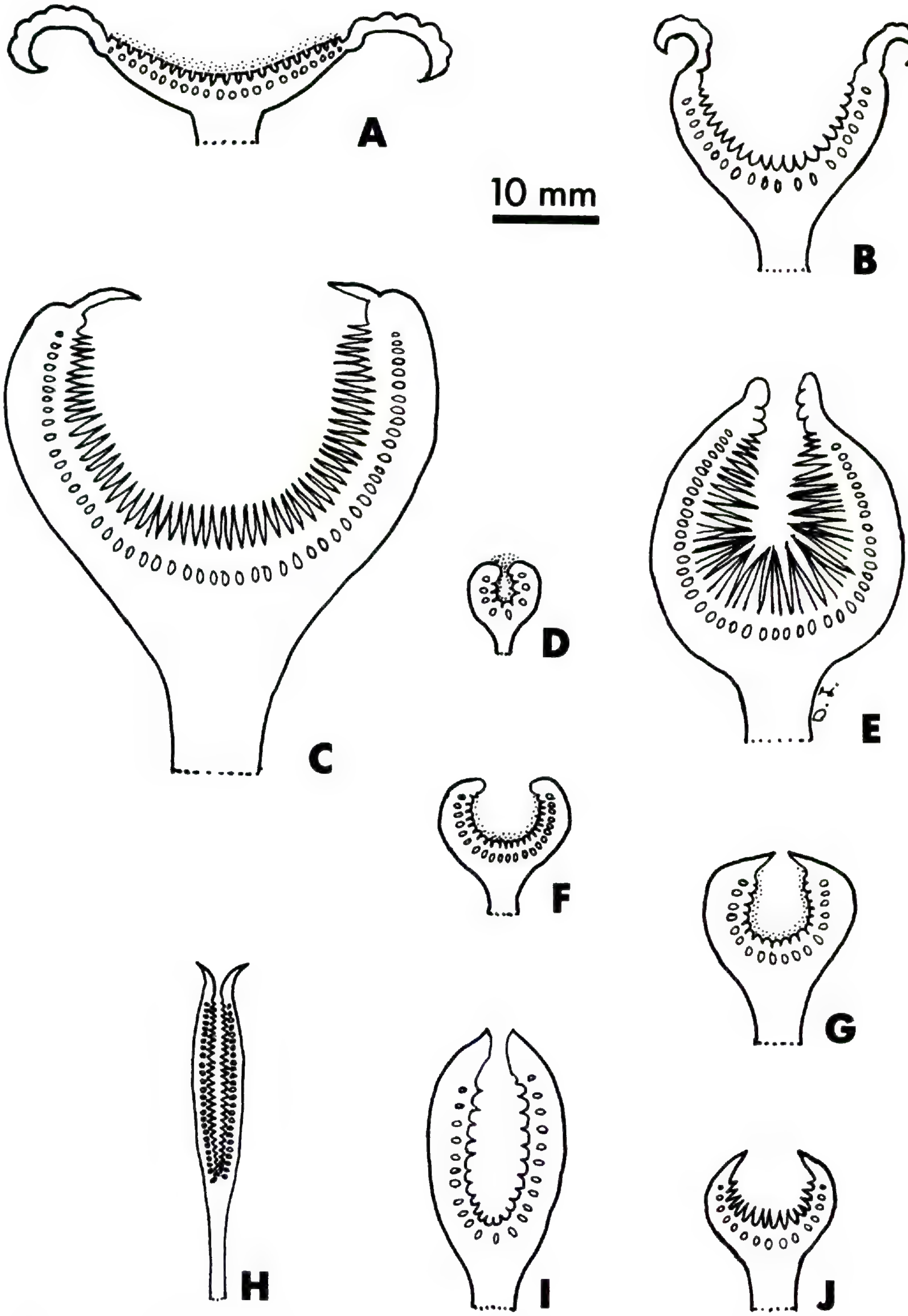


FIGURE 15. Schematic longitudinal sections through gynoecious floral receptacles of some *Tambourissa* species.—A. *T. peltata.*—B. *T. cordifolia.*—C. *T. ficus.*—D. *T. purpurea.*—E. *T. sieberi.*—F. *T. comorensis.*—G. *T. elliptica.*—H. *T. alaticarpa.*—I. *T. quadrifida.*—J. *T. pedicellata.* Stippled areas represent mucilaginous compitum. Drawn to approximate scale.

gynoecious receptacles of *T. quadrifida* are cylindrical-ellipsoid, and those of *T. floricostata* bear four lateral, longitudinal ridges. The external receptacular surface in the genus ranges from glabrous (e.g., *T. tetragona*) to densely velutinous (e.g., *T. sieberi*) or corky (e.g., *T. tau*).

The gynoecious bud apex in *Tambourissa* generally bears several pairs of minute, decussate obtuse or deltoid, scale-like tepals. Two pairs are usually visible externally in most species, and these are sometimes fused into an apicule (e.g., in *T. sieberi, T. tau*). In *T. purpurea* there are usually five pairs; the innermost are enclosed in the floral cup and intergrade into the carpels (Endress, 1980b; as *T. religiosa*). In several of the Comorean species in Group 2 (*T. comorensis,* Figs. 15F, 17B; *T. kirkii*; and *T. leptophylla*) where the gynoecious receptacle remains open during the entire floral development, the tepals are apparent only during the very young stages. This is an unusual feature within the genus, and could represent either a highly advanced character or, alternatively, a transitional stage between the open, discoid receptacles of *Ephippiandra* and the closed buds of most *Tambourissa* species. At floral anthesis, the receptacles of most species generally split open by shallow (e.g., *T. purpurea*) to deep (e.g., *T. peltata*) longitudinal fissures between the tepals, forming a number of subequal lobes ranging from four in most species (e.g., *T. cordifolia,* Fig. 42G, H) to as many as eight or ten in *T. ficus* (Fig. 15C) and *T. tau* (Fig. 39E). The sterile internal surface of the lobes may be pubescent (e.g., *T. moheliensis,* Fig. 36E) or glabrous (*T. tau*). Inner lobes of *T. peltata,* and to a lesser degree *T. cordifolia,* are sculptured with longitudinal ridges or lines, somewhat verrucose in the former species and bearing stomata in both species (Endress & Lorence, 1983). Position of the lobes at anthesis ranges from incurved (e.g., *T. pedicellata,* Fig. 15J), or erect (e.g., *T. hildebrandtii*), to spreading-reflexed (e.g., *T. peltata*; Figs. 15A, 17E). The colorful, everted lobes of *T. peltata* have assumed the function of the perianth.

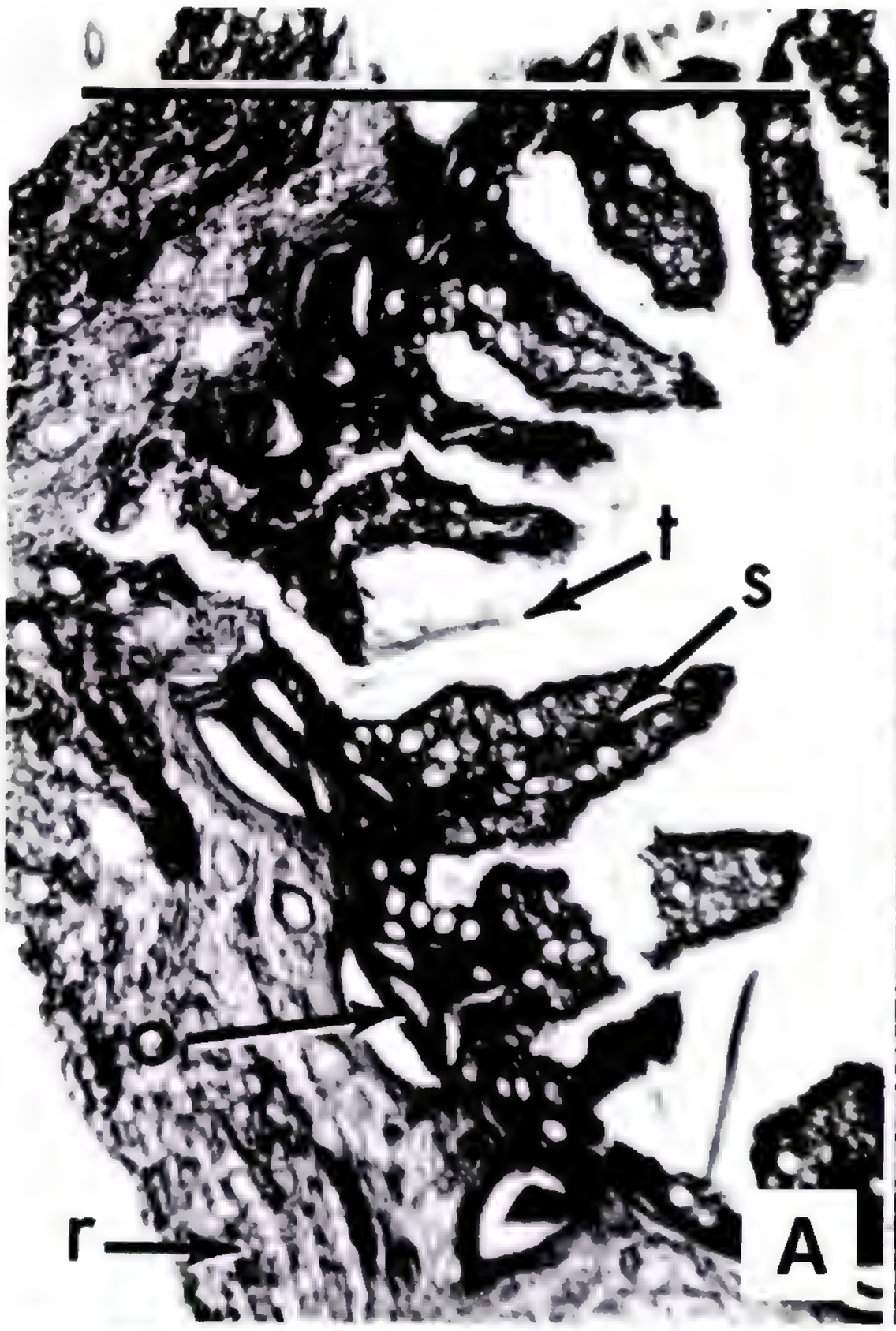
The carpels of *Tambourissa* are immersed in and united with the receptacle wall and are therefore inferior and syncarpous in a morphological sense (Endress, 1979, 1980b, 1982), not embedded in sockets as stated by Baillon (1871) and Corner (1976). Each carpel is unilocular with a solitary, bitegmic, anatropous ovule (amphitropous in *T. decaryana, T. nosybensis*). The two species formerly included in *Phanerogonocarpus* (*T. alaticarpa* and *T. longicarpa*) also possess this type of carpel (Fig. 16A). The inner receptacle surface may be glabrous (e.g., *T. tau*; Fig. 16C) or interspersed with dense tufts of short, simple lignified trichomes (e.g., *T. sieberi*; Fig. 16D).

The number of carpels varies greatly between species, is proportional to the size of the receptacle, and provides a good, species-specific character (Table 6). For example, fresh flowers of *T. purpurea* are only 5–6 mm diam. and have 35–70 carpels, whereas those of *T. ficus* are 35–40 mm diam. and have ca. 1,000–2,000 carpels. Size and shape of the styles are constant and often species-specific features, varying greatly within the genus. Styles of *T. peltata* (Fig. 16B) are short (ca. 0.5 mm long), crowded, and obtusely columnar. Those of *T. tau* (Fig. 16C) are longer (ca. 2–3 mm), free and setose, whereas in *T. sieberi* (Fig. 16D) they are 3–4 mm long, setose and coalescent. A canal was found to run obliquely upward from the ovule before opening at the base of the style in all 31 species examined in this study. This canal has been termed the "ventral slit" by Endress (1980b) and allows passage of the pollen tube for fertilization.

Pollen tube transmission in *Tambourissa* does not occur through the stylar tissue; rather, the site of transmission has shifted to the exterior of the style as in many other genera in the Monimiaceae (Endress, 1979, 1980b). In many species the entire external stylar surface is secretory, producing a mucilaginous exudate through which the pollen tubes grows until encountering the stylar canal and passing through it directly to the ovule. Traces of this mucilage can be seen in Figures 13E and 16C.

A further specialization is a massive mucilage production forming a thick layer lining the floral cup (e.g., *T. peltata*; Figs. 15A, 17E). This "extragynoecial compitum" functionally links and interconnects all the carpels (Endress, 1980b, 1982), enabling pollen grains deposited in one place to cross over and grow to any other carpel, thereby maximizing efficiency of the pollen. It is analogous to the usual intragynoecial compitum (transmitting tissue) in syncarpous gynoecia (Carr & Carr, 1961). The mucilage may also have a nectar function (see chapter on Floral Biology).

In *Tambourissa purpurea,* the extra-carpellary, stigmatic secretory epidermis covers not only the surface of the carpels but also the entire inner orifice of the floral cup including the inner tepals. Termed a "hyperstigma" by Endress (1979,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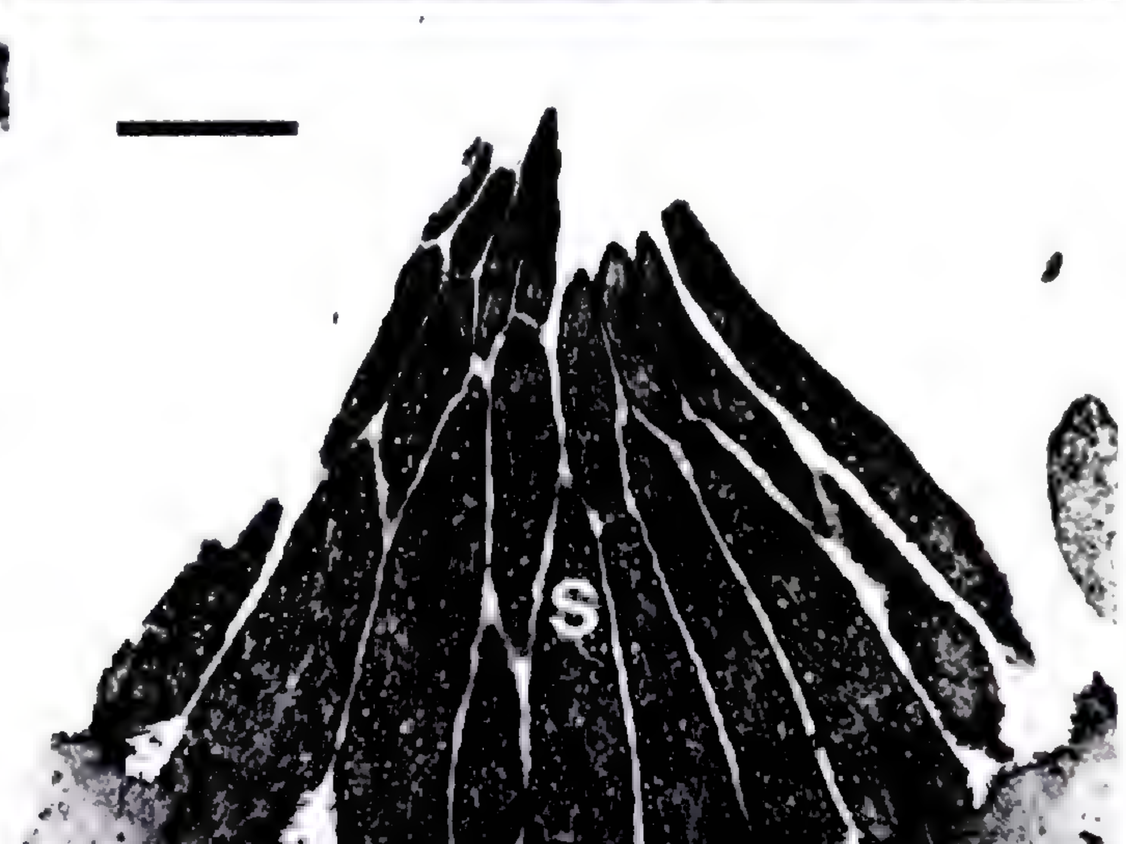
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1980b; as *T. religiosa*), this unique floral construction is the culmination of floral specialization in Monimiaceae. In addition to *T. purpurea* it also occurs in *T. elliptica* and *T. crassa* (Lorence, pers. observ.), as well as *Wilkiea, Kibara,* and *Hennecartia.* (Endress, 1980b). In *T. purpurea,* a mucilaginous plug completely occludes the floral pore and forms a continuous layer extending down to the carpels and functions as the pollen reception and transmission site. In *T. crassa* and *T. elliptica,* the orifice is only occluded early in anthesis, but the mucilage otherwise completely lines the floral cup. A conspicuous mucilaginous exudate was also observed in fresh or rehydrated flowers of *T. decaryana, T. comorensis, T. longicarpa, T. madagascariensis, T. nosybensis, T. peltata,* and *T. beanjadensis* (Table 7).

Each *Tambourissa* carpel is supplied by a single vascular bundle dorsal to the ovule which runs into the style for much of its length. The carpels and receptacular ground tissue of each species characteristically contain varying proportions of one or more types of the following idioblasts: oil cells; tanniferous cells; stone cells. Amount and type of each provide useful, species-specific characters (Table 7).

Androecious flowers of all species of *Tambourissa* are globose to subglobose and closed in bud, usually bearing apically two external pairs of small to minute, free to fused tepals, and one or more additional pairs enclosed in the receptacle. The presence of tepals (as "staminodes") on inner receptacle lobes of the species formerly included in *Phanerogonocarpus* occurs in many species of *Tambourissa* and does not serve to distinguish the two genera as stated by Cavaco (1957c). The external receptacle surface is comparable to that of the gynoecious flower, ranging from glabrous to densely pubescent or corky. Male floral size shows great intraspecific variation, but is often comparable to that of the gynoecious receptacle. Two of the Comorean species, *T. kirkii* and *T. moheliensis* (Figs. 18D, 36D, E) have androecious receptacles that are much smaller than the gynoecious ones, however. The number of stamens is likewise proportional to receptacle size, and is generally somewhat less than the number of carpels in a given species (Table 6). To cite extremes, fresh androecious buds of *T. purpurea* are 5–6 mm diam. with 20–32 stamens, whereas those of *T. ficus* are 45–50 mm diam. and contain ca. 900–1,800 stamens, making it the largest androecious flower in the family!

At anthesis, androecious flowers of most *Tambourissa* species split open by longitudinal fissures between the tepals into generally four or sometimes five (range three to seven) subequal, valvate lobes. The number of lobes and degree to which they split and reflex provide useful, species-specific characters. For example, lobes of *T. pedicellata* (Figs. 17C, 18F) are shallowly fissured, incurved, and scarcely open more than halfway. Those of *T. amplifolia* (Fig. 18B) split about halfway and open flat, whereas those of *T. quadrifida* (Figs. 18I, 19B) split deeply to the base and recurve completely. In some, including *T. purpurea* (Fig. 18E) and Comorean species such as *T. moheliensis* (Fig. 18D), the floral cup merely splits by shallow fissures and remains relatively closed and globose. An extreme form occurs in *T. gracilis* and *T. paradoxa,* which do not split at all; a small pore flanked by tepals provides the only access to the stamens. Such minute, closed flowers and very large, open flowers probably represent highly specialized, extreme forms derived from a more generalized type, perhaps similar to that of *T. pedicellata.*

Stamens of many *Tambourissa* species (e.g., *T. pedicellata*; Fig. 18F) consist of a distinct, broad filament and two lateral, bisporangiate, longitudinally dehiscent, extrorse loculi beyond which the connective is often slightly prolonged. This relatively unspecialized type resembles those found in *Decarydendron* and some species of *Ephippiandra.* Other species of *Tambourissa* display a number of extreme and highly specialized trends. One trend is towards extreme staminal elongation and prolongation of the connective, e.g., in *T. capuronii* (Fig. 18C) with stamens 6–8 mm long. In *T. tau* (Fig. 18H), the loculi occur on extended lateral arms of the connective in the form of a "T." The loculi of *T. ficus* (Fig. 18G) have shifted to an abaxial position with the filament and prolonged connective thickened. In other species such as *T. amplifolia* (Fig. 18B) and *T. peltata* (Figs. 17D, 18A), the loculi are often apically confluent and dehiscence

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FIGURE 16. Styles and carpels of some *Tambourissa* species, longitudinal sections.—A. *T. longicarpa, Capuron 8775-SF* (P).—B. *T. peltata, Lorence 2555* (MO).—C. *T. tau, Lorence 2953* (MO).—D. *T. sieberi, Lorence 2250* (MO). Bars equal 1 mm. c = canal leading to ovule; m = mucilaginous exudate; o = ovule; r = receptacular ground tissue; s = style; t = trichome.

TABLE 6. Selected floral morphological features of *Tambourissa* species according to Group.

Species	Group	Sex	Androecious Flower	Stamens			Gynoecious Flower		Styles	
			Shape at Anth.	No. (ca.)	Connective	Loculi	Shape	Orifice	No. (ca.)	Shape
T. thouvenotii	1A	monoec.	4-fid, flat	50–100	prol.	free	napiform-depressed	4-lobed	100–150	conical
T. trichophylla	1A	monoec.	4-fid, flat	±100	prol.	free	subglobose	4-lobed	100	conical
T. uapacifolia	1A	dioec.?	4-fid, flat	±100	apic.	free	?	?	?	conical
T. decaryana	1B	dioec.?	? ?	?	?	?	napiform-depressed	4–5-lobed	200–300	conical
T. hildebrandtii	1B	monoec.	4-fid, flat	75–90	prol.	free	napiform-subglobose	4-lobed	150–200	conical
T. humbertii	1B	dioec.?	? ?	?	?	?	napiform-depressed	4(–5)-lobed	500	ovoid
T. nitida	1B	monoec.	? ?	60	apic.	free	napiform-turbinate	?	200†	conical
T. nosybensis	1B	monoec.?	4-fid, flat	70	apic.	free	discoid-patelliform	4-lobed	400	conical
T. floricostata	1C	monoec.	4-fid, incurved	16–22	apic.	free	globose-depressed	subcirc.	?	conical
T. parvifolia	1C	monoec.	4-fid, flat	50–60	apic.	free	subglobose-napiform	subcirc.	200†	conical
T. beanja-densis	2A	monoec.	4–5-fid, flat	36	non-prol.	confl.	globose-napiform	4-lobed	200	conical
T. comorensis	2A	monoec.	4-fid, flat	125–150	non-prol.	free	patellif.-urceol.	circul., entire	200†	columnar
T. crassa	2A	dioec.	4–5-fid, ± flat	125–250	non-prol.	confl. (free)	subglobose-depressed	4(–8)-lobed	200†	columnar
T. elliptica	2A	monoec.	4-fid, flat	65–300	non-prol.	free (confl.)	globose-depressed	4-lobed	150–200†	columnar

TABLE 6. Continued.

Species	Group	Sex	Androecious Flower	Stamens			Gynoecious Flower		Styles	
			Shape at Anth.	No. (ca.)	Connective	Loculi	Shape	Orifice	No. (ca.)	Shape
T. leptophylla	2A	monoec.	4-fid, flat	80–90	apic.	free	globose-depressed	circul., entire	300–600	conical
T. madagascariensis	2A	dioec.?	4-fid, flat	200	apic.	free	subglobose-depressed	circul., entire	200†	columnar
T. kirkii	2B	monoec.	3-fid, subglobose	50?	prol.	free	patellif.-urceol.	circul., entire	200	conical
T. paradoxa	2B	dioec.?	globose, with small pore	40–50	prol.	free	?	?	?	?
T. capuronii	3	monoec.	4(–5)-fid, flat	300	prol.	free	napiform-depressed	±6-lobed	200†	conical
T. moheliensis	3	monoec.	4-fid, closed, subglobose	50	prol.	united basally	napiform-depressed	4-lobed	100–200	conical
T. gracilis	4	dioec.?	globose, with small pore	50	non-prol.	confl.	?	?	?	conical
T. purpurea	4	monoec.	globose, with small 3–4-lobed pore	20–32	non-prol.	confl.	globose	small, 3–4-lobed	35–70	columnar
T. religiosa	4	monoec.	closed? 4-lobed	50–75	apic. (non-prol.)	free-conniv.	napiform-depressed	4-lobed	300	conical
T. amplifolia	5	monoec.	4-fid, flat	100–250	non-prol.	confl.	napiform-discoid	4-lobed	300	conical
T. cocottensis	5	monoec.	4–7-fid, flat	150–200	prol.	free	napiform-depressed	5–7-lobed	150–200	setose
T. cordifolia	5	dioec.	4-fid, flat	300–400	non-prol.	free-confl.	napiform-urceolate	4-lobed	100–400	conical

TABLE 6. Continued.

Species	Group	Sex	Androecious Flower	Stamens			Gynoecious Flower		Styles	
			Shape at Anth.	No. (ca.)	Connective	Loculi	Shape	Orifice	No. (ca.)	Shape
T. pedicellata	5	monoec.	4(–6)-fid, half closed	50–70	non-prol.	free	subglobose	4–7-lobed	60–180	conical
T. tau	5	monoec.	4–5-fid, flat	100–150	apic. (non-prol.)	free	subglobose-urceolate	5–10-lobed	80–100	setose
T. tetragona	5	dioec.?	?	?	?	?	napiform-depressed	4-lobed	200	conical
T. bathiei	6	monoec.	3–4-fid, flat	350–450	non-prol.	free-confl.	globose	?	200†	conical
T. sieberi	6	monoec.	(4–)5-fid, flat	100–140	apic. (non-prol.)	free	globose	subcirc., small	850–875	setose
T. perrieri	7	monoec.	4-fid, flat-recurved	150–200	non-prol.	free	obovoid-obpyrif.	4-lobed, small	200	conical
T. quadrifida	7	monoec.	4-fid, flat-recurved	300–500	non-prol.	free	oblong-ellipsoid	3–4-lobed, very small	200–300	conical
T. alaticarpa	8	monoec.	4-fid, flat	38	non-prol.	free	cylindrical	6–8-lobed	250–300	conical
T. longicarpa	8	monoec.	4-fid, flat	40–50	prol.	free	cylindrical	4–6-lobed	500	conical
T. castri-delphinii	9	dioec.?	4–5-fid, flat-recurved	200–300	non-prol.	confl.	napiform-depressed	X-shaped	800–900	conical
T. ficus	9	monoec.	5–7-lobed, urceolate or flat	900–1,800	prol.	free (±unilateral)	urceolate	6–8-lobed	1,000–2,000	setose
T. peltata	9	dioec.	4–5-fid, flat-recurved	200–400	apic. (non-prol.)	free-confl.	discoid	4–7 flat lobes	400–500	flat, columnar (crowded)

is continuous. In *T. purpurea* (Fig. 18E), locular confluence is accompanied by an extreme staminal shortening and broadening, the resulting stamen being sessile or subsessile (0.7–1.2 mm long) with a single, crescentiform loculus which dehisces apically (Endress, 1980b; as *T. religiosa*) as in some species of *Ephippiandra*. However, basal fusion of the loculi occurs only in *T. moheliensis* (Fig. 18D), and also in some (but not all) stamens of *T. cordifolia* (Fig. 42C–E).

Anatomically, the androecious receptacle is similar to that of the gynoecious one. A single vascular bundle supplies each stamen (e.g., in *T. tau*). The same types of idioblasts are often found in the androecious flowers as in the gynoecious ones, most commonly oil and tanniferous cells. Stone cells, however, tend to be less abundant or lacking in the androecious flowers, e.g., *T. purpurea* (Endress, 1980b; as *T. religiosa*). Their greater abundance in gynoecious flowers and fruits suggests they may play a role in protecting the developing ovules from predation.

Floral color is relatively constant in many species, but quite variable in others (Table 8) which often have two color morphs. Flower color is always constant on a given individual and frequently constant within a local population. In *T. quadrifida,* however, both color morphs were observed in a single population at Yemen Valley, Mauritius. Incidentally, floral odor was found to be quite constant for each species and provides a diagnostic field character. Floral morphology, color, and odor all appear to be related to pollination syndromes (see discussion under Floral Biology).

In summary, floral size and morphology, including number, structure, and color of stamens in the androecious flowers and number, structure, and color of the styles in the gynoecious flowers are distinctive for most species of *Tambourissa.* These features provide some of the most taxonomically useful characters in the genus and should be recorded in the field notes. As flowers lose their shape upon drying, supplementary collections of flowers in alcohol should also be made whenever possible, as well as a photographic record. For a more detailed study of the floral morphology and anatomy of *Tambourissa,* see Endress and Lorence (1983).

FRUITING RECEPTACLE AND CARPELS

The seed-like fruiting carpels of all the genera for which information is available are fundamentally similar in being drupaceous and indehiscent with a lignified endocarp, an abundant, oily endosperm, and a small embryo. While much larger in fruit, the shape of the receptacle and the carpels' position largely correspond with their shape and position in flower; i.e., significant generic differences exist. Also, the thick, pitted, bony white endocarp of *Monimia* (Monimioideae sensu Thorne, 1974) differs conspicuously from the thinner, finely sculptured, brownish, horny endocarps of the genera in Mollinedioideae (e.g., *Ephippiandra* and *Tambourissa*; unknown in *Decarydendron*).

Fruiting receptacles of all three species of *Monimia* are similarly subglobose to ovoid, enclosing from one to 12 free, seed-like drupaceous carpels. On herbarium labels these are often mistaken for multiple-seeded fruits. Fruiting receptacles of *Monimia* are strikingly similar to those of *Palmeria* (Corner, 1976; Endress, 1980b). At maturity the receptacle splits longitudinally from the apex into three to six irregular, valvate lobes that open to reveal the bright orange fruiting carpels set against the pinkish red receptacular surface (Figs. 14C, D, 19C). Birds appear to be the effective seed vectors for *M. ovalifolia* in Mauritius (Lorence, pers. observ.), and also for the species of *Monimia* in Réunion (A. Rolland, pers. comm.).

The indehiscent carpels of *Monimia* consist of a lignified, bony endocarp enveloped by a soft, orange, aril-like outer coating apparently composed of two distinct elements. The outermost is an enation extending downward from the stylar base over the apical portion of the carpel and forming a cap-like structure covering the lateral portions of the carpel, while leaving the dorsal and especially the ventral portion exposed (Fig. 19A, B, D). This outgrowth contains numerous oil cells and appears to represent an arilloid structure. The inner layer consists of the mesocarp proper which completely surrounds the endocarp, but is thickest basally (Fig. 19A, B, D). It is also orange but lacks the oil cells of the former. An analogous situation occurs in the neotropical *Siparuna* (Corner, 1976; Endress, 1973), and has been termed a "carpellary aril" or "stylar aril" respectively by these authors. Further studies on the development of *Monimia* carpels are in progress (Endress & Lorence, in prep.).

The endocarp of *Monimia* is whitish, irregularly ovoid-compressed, longitudinally crested and apically mucronate with the micropyle passing through the base of the beak. The wall is hard and bony, ca. 0.5–2 mm thick (probably adequate to survive passage through a bird's gut),

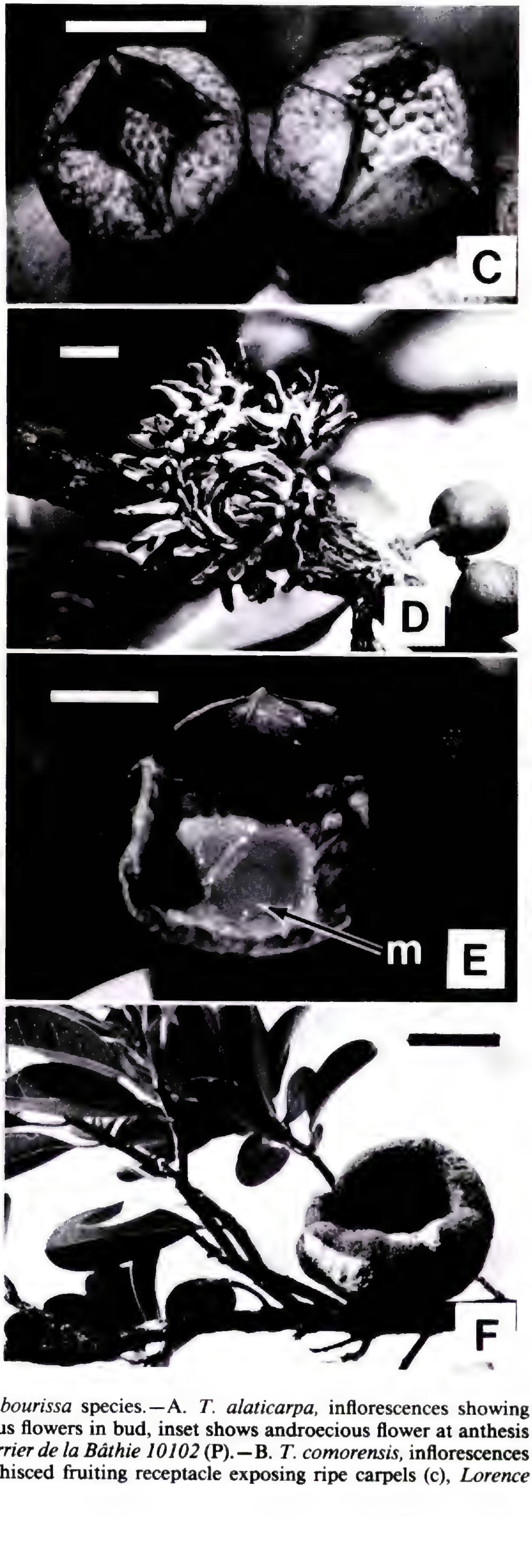


FIGURE 17. Flowers and fruits of some *Tambourissa* species.—A. *T. alaticarpa,* inflorescences showing terminal gynoecious flowers and lateral androecious flowers in bud, inset shows androecious flower at anthesis and longitudinally sectioned gynoecious flower, *Perrier de la Bâthie 10102* (P).—B. *T. comorensis,* inflorescences with androecious and gynoecious flowers, and dehisced fruiting receptacle exposing ripe carpels (c), *Lorence*

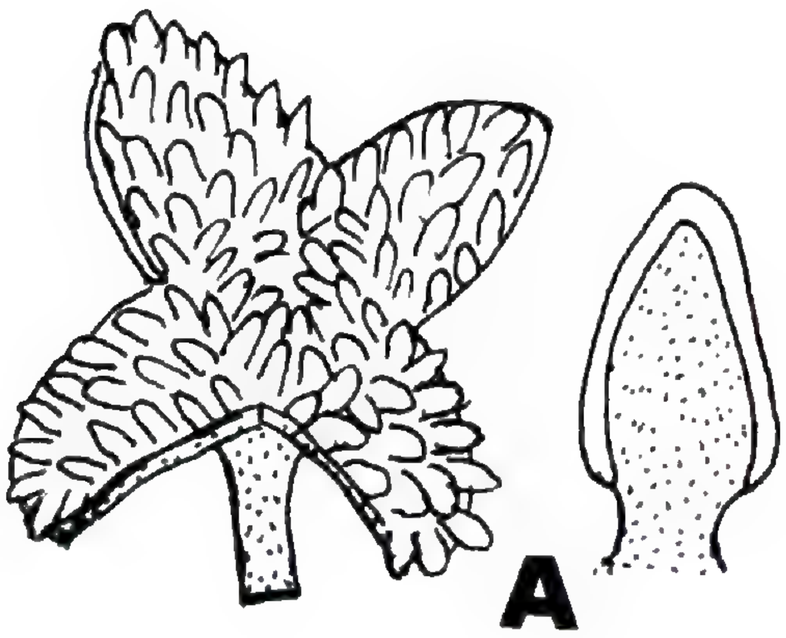
TABLE 7. Selected floral anatomical features of *Tambourissa* species according to Group. Data given for both androecious and gynoecious flowers, except where noted. ± indicates presence of a small amount.

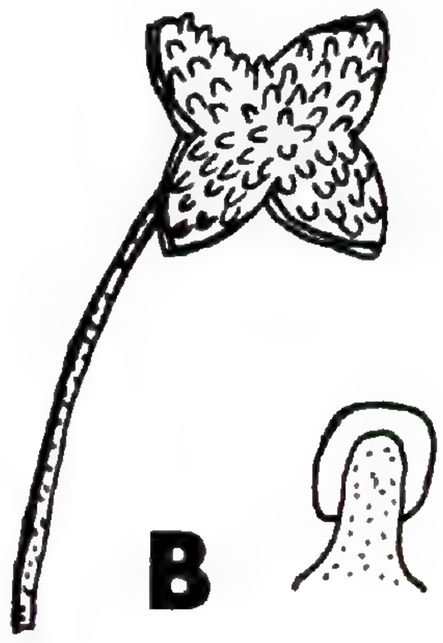
Species	Group	Tanniferous Idioblasts	Stone Cells (Sclerids)	Oil Cells	Mucilaginous Compitum (Gynoecious)
T. thouvenotii	1A	+	−	−	−
T. trichophylla	1A	−	+	+	−
T. uapacifolia (♂)	1A	−	−	+	?
T. decaryana	1B	−	+	+	+
T. hildebrandtii	1B	+	−	+	−
T. humbertii	1B	−	−	+	−
T. nitida	1B	+	−	+	?
T. nosybensis	1B	−	+	+	+
T. floricostata	1C	+	−	+	?
T. parvifolia	1C	−	+	+	?
T. beanjadensis	2A	−	+	+	±
T. comorensis	2A	−	+	+	±
T. crassa	2A	−	−	+	+
T. elliptica	2A	±	+	−	+
T. leptophylla	2A	−	+	+	−
T. madagascariensis	2A	+	+	+	±
T. kirkii	2B	?	?	?	− (?)
T. paradoxa (♂)	2B	−	+	+	?
T. capuronii	3	+	+	−	−
T. moheliensis	3	+	+	±	−
T. gracilis (♂)	4	−	−	+	?
T. purpurea	4	+	+	−	+
T. religiosa	4	+	+	−	− (?)
T. amplifolia	5	+	+	+	−
T. cocottensis	5	+	+	−	−
T. cordifolia	5	+	+	−	−
T. pedicellata	5	−	+	+	−
T. tau	5	+	+	+	−
T. tetragona	5	+	−	+	−
T. bathiei	6	+	+	+	−
T. sieberi	6	−	+	+	−
T. perrieri	7	−	+	+	−
T. quadrifida	7	+	+	−	−
T. alaticarpa	8	+	+	−	−
T. longicarpa	8	+	+	+	±
T. castri-delphinii	9	+	+	+	−
T. ficus	9	+	+	+	−
T. peltata	9	+	+	−	+

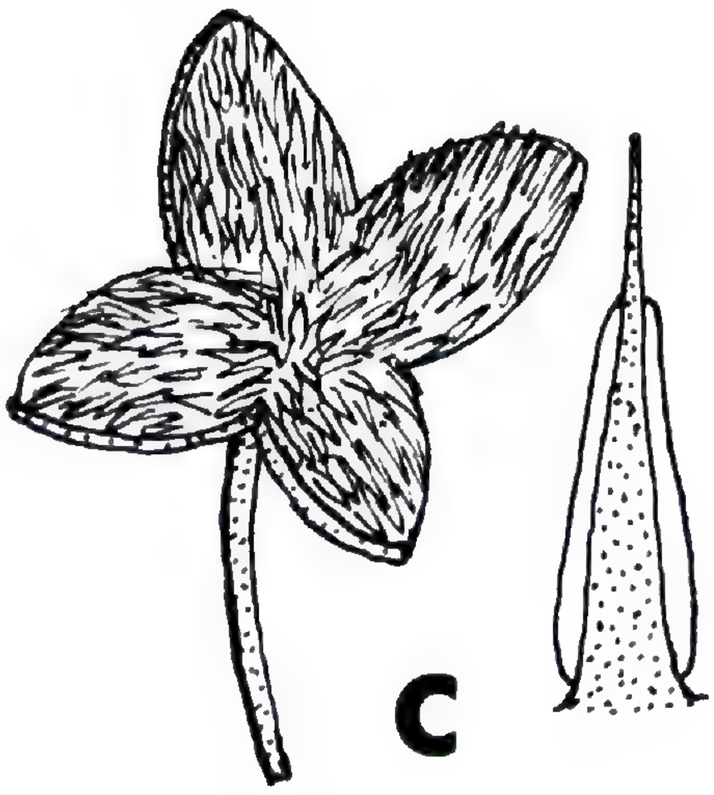
and consists of many layers of contiguous sclerids. The endocarp surface is externally deeply pitted as in *Peumus* and *Siparuna*. Surface sculpturing ranges from foveate to reticulate or sulcate, varying even within a single species. Inside, a thin single-layered tegmen composed of elongated, rectangular cells encloses the abundant, oily endosperm. The small embryo is situated near the micropyle (Fig. 19A) and has slightly divaricate cotyledons. Germination of both *M.*

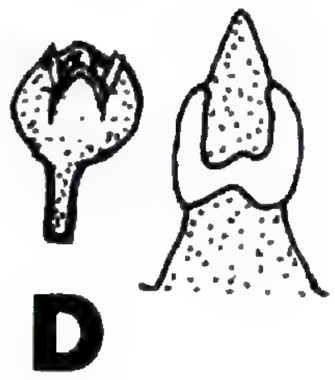
←

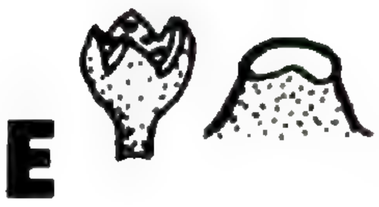
2870 (MO).—C. *T. pedicellata,* gynoecious (left) and androecious (right) flowers at anthesis, *Lorence 2384* (MO).—D. *T. peltata,* androecious flower at anthesis and two androecious buds, Perrier Nature Reserve, Mauritius (R. E. Vaughan, unvouchered photo).—E. *T. peltata,* newly opened gynoecious flower, note copious mucilaginous exudate (m) on gynoecial disc, *Lorence 2555* (MO).—F. *T. peltata,* submature fruiting receptacle on branch, *Lorence 2197* (MO). Bars equal 10 mm in A, C–E, and 50 mm in B, F.

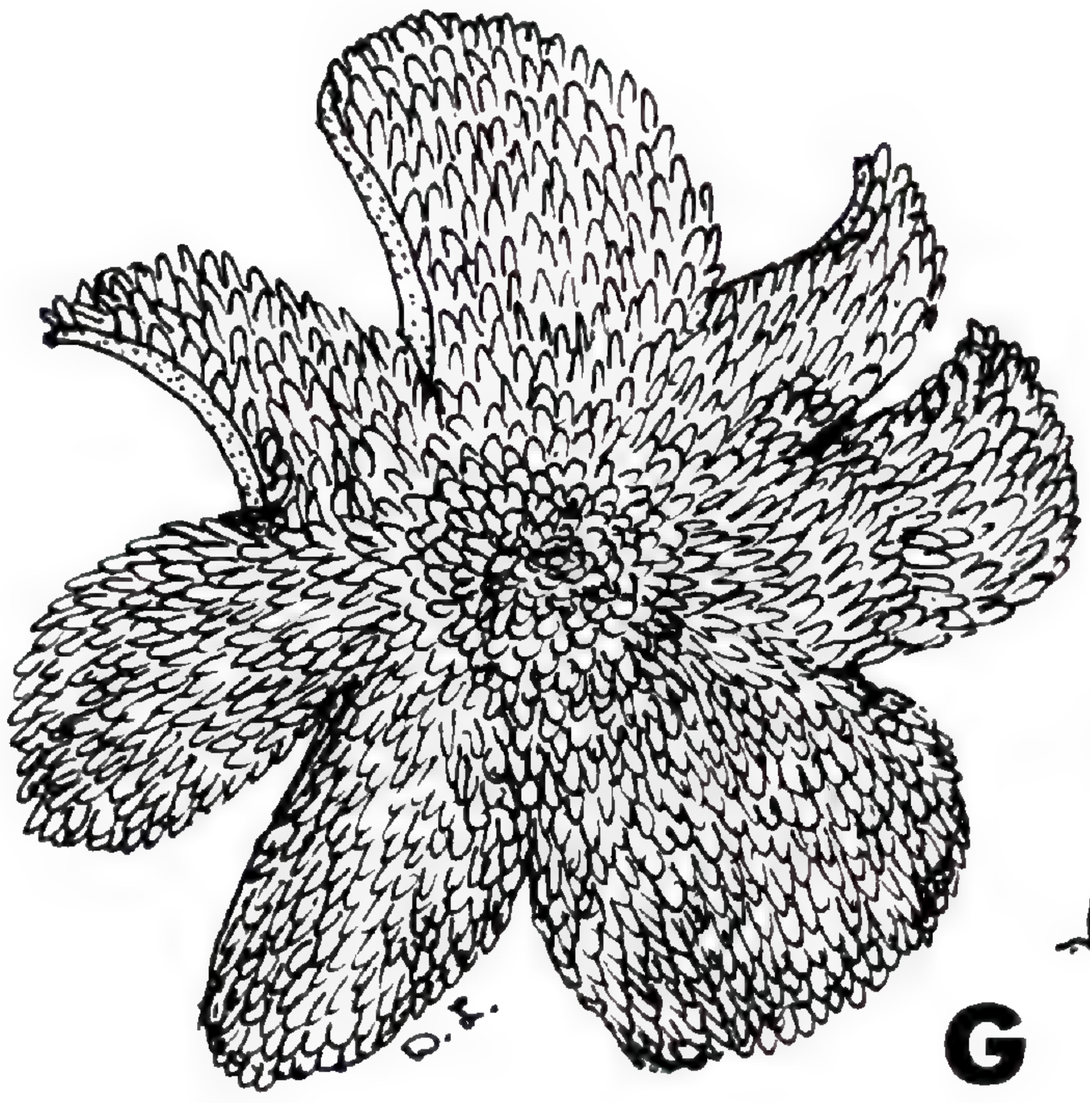


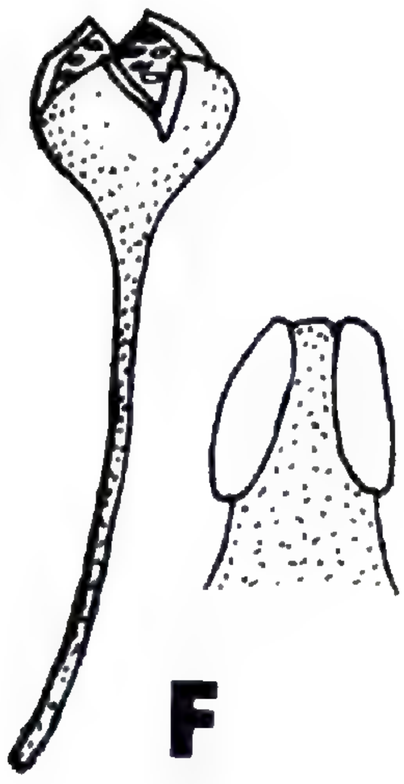


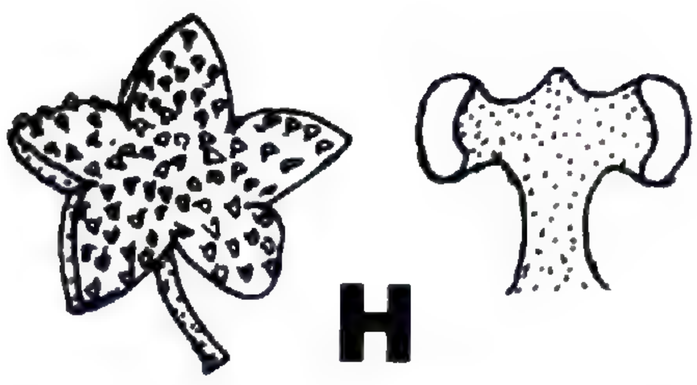












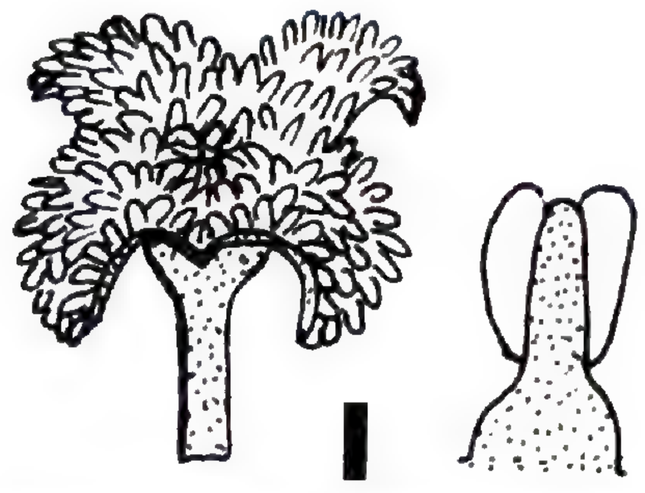


FIGURE 18. Androecious flowers and stamens of some *Tambourissa* species, drawn to approximate scale.—A. *T. peltata.*—B. *T. amplifolia.*—C. *T. capuronii.*—D. *T. moheliensis.*—E. *T. purpurea.*—F. *T. pedicellata.*—G. *T. ficus.*—H. *T. tau.*—I. *T. quadrifida.* Bar equals ca. 10 mm for flowers and ca. 1 mm for stamens.

TABLE 8. Floral color morphs of individuals of some species of *Tambourissa* from Mauritius and Réunion (inner receptacle surface, stamens or styles).

Species	Androecious Flower Color	Gynoecious Flower Color
T. amplifolia	white	orange; pale yellow
T. cordifolia	white	pink; purple-red
T. crassa	pale yellow; dark purple-red	pale yellow-green; dark purple-red
T. elliptica subsp. *elliptica*	white; pink	pale yellow-green; pink
T. ficus	white; purple-red	yellow-pink
T. peltata	purple-red; salmon pink	lobes purple-red, disc orange
T. quadrifida	orange; red	greenish white; reddish pink
T. sieberi	pale yellow; purple-red	pale yellow-green; purple-red
T. tau	greenish white; purple-red	purple-red

ovalifolia and *M. rotundifolia* seeds took over four months and viability was quite low, ca. 10–15%.

Fruiting carpels of *Decarydendron* are unknown (Cavaco, 1959). Because its flowering carpels are free and subsessile on the receptacular surface, the fruiting carpels may resemble those of *Ephippiandra* in being free and exposed on the receptacle, but probably lack a basal cupule and are sessile or shortly stalked as in *Hedycarya* or *Mollinedia*.

Mature fruiting receptacles of *Ephippiandra* (including *Hedycaryopsis*) are discoid, flat to convex, fleshy and red when fresh, and bear ca. 10–75 free, ovoid to ellipsoid carpels ca. 7–12 mm long. Each is partly surrounded basally for about one-third to one-half its length by a cupule (Fig. 14H) derived from the receptacle. The mature carpels are composed of a thin, fleshy green exocarp which turns black on ripening and surrounds the thin, pale brown, horny endocarp. The endocarp surface is smooth and finely scrobiculate as in *Tambourissa* and encloses a copious, fleshy endosperm.

As in the other genera, fruiting receptacles of *Tambourissa* (including *Phanerogonocarpus*) are many times larger than the flowers but otherwise similar in shape, ranging from flat and discoid (e.g., some *T. peltata* fruits), or somewhat open and cupuliform in the majority (e.g., Figs. 17B, F, 42J), to ellipsoid and closed with a small orifice in *T. quadrifida*, or cylindrical with four to five prominent external ridges in *T. alaticarpa* and *T. longicarpa*. The majority are corky brown externally, but may be smooth and dark (reddish when fresh) in *T. purpurea* and *T. religiosa*. Most have an internal cavity, but some fruits of *T. hildebrandtii* are almost solid. The styles persist in fruit and line the cavity, providing important diagnostic features as to their size, shape, and number. Other taxonomically useful features of the fruiting receptacle are its position on the plant (on the trunk, branches, or terminal), whether solitary or in clusters, its size, shape, and the proportional size of the orifice.

At maturity the receptacle splits open irregularly, exposing the numerous, bright red-orange

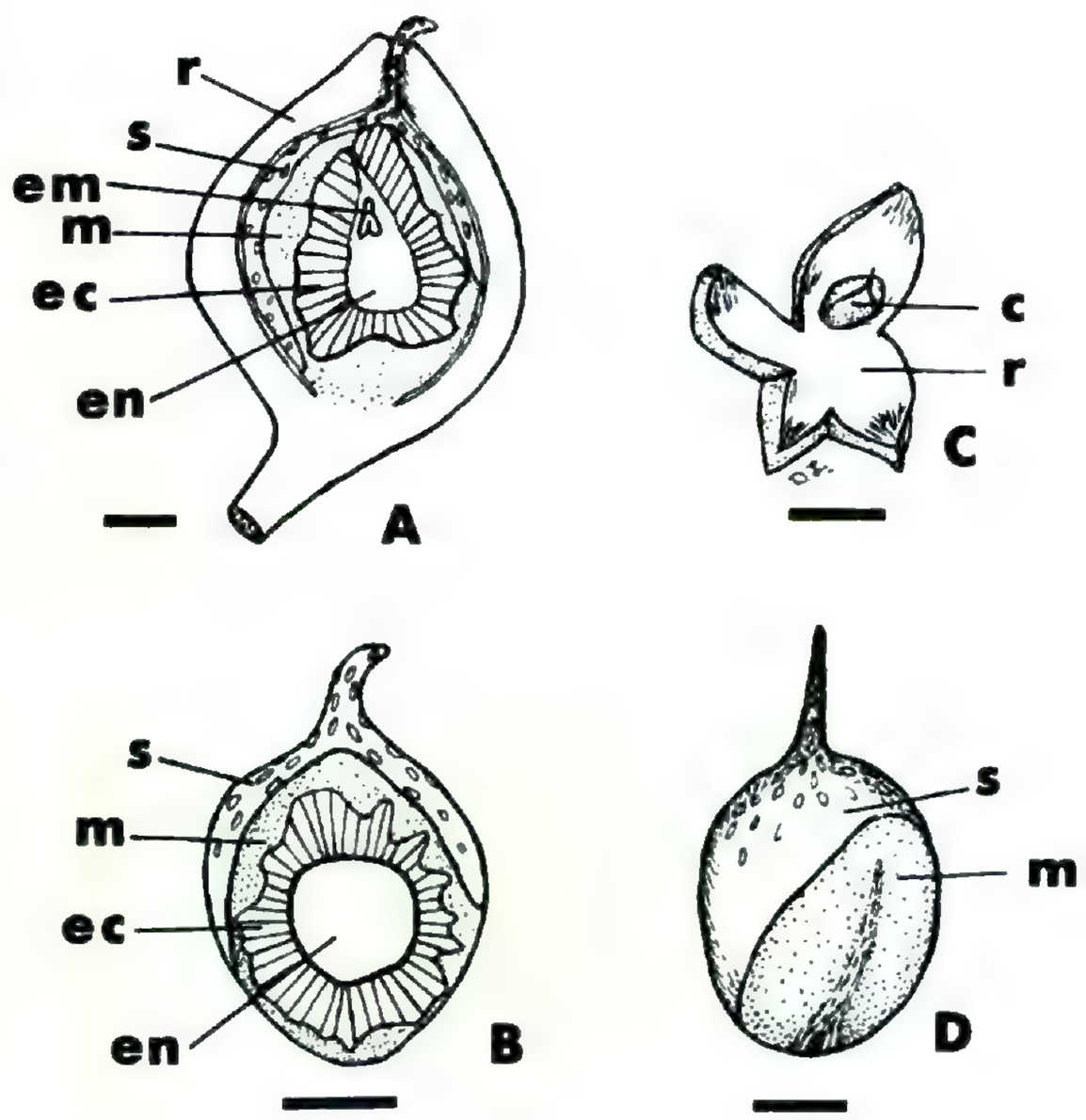


FIGURE 19. *Monimia* fruiting receptacles and carpels.—A. *M. ovalifolia*, submature fruiting receptacle with single carpel, longitudinal section, *Lorence 2350* (MO).—B. *M. ovalifolia*, mature fruiting carpel, longitudinal section, *Lorence 2350* (MO).—C. *M. amplexicaulis*, ripe receptacle split open to reveal single carpel, *Lorence 2503* (MO).—D. *M. amplexicaulis*, ripe fruiting carpel, abaxial view, *Lorence 2503* (MO). Bars equal 2 mm in A, B, D, and 10 mm in C. c = carpel; ec = endocarp; em = embryo; en = endosperm; m = mesocarp; r = receptacle; s = stylar aril.

carpels which separate from the pale orange receptacular ground tissue (Fig. 17C). In *Tambourissa cordifolia* (*Lorence 2630,* MO), the receptacle consists of parenchymatous ground tissue intermixed with sheets and columns of tanniferous cells and brachysclerids comprising nearly half the total tissue mass. In carpels of *T. cordifolia* the mesocarp is composed of parenchymatous cells containing numerous orange plastids interspersed with abundant oil cells and has a sweet taste when fresh (D. Lorence, pers. observ.). Beneath the mesocarp lies a horny, brown endocarp with a smooth, finely sculptured surface composed of numerous subspheroidal to cuboidal, lignified sclerids united into longitudinal bands and overlain by a single outer layer of flat, discoid sclerids. Beneath this lies an endotesta of elongated, annular tracheids three to four cell layers thick, and finally a unicellular tegmen of cuboidal cells surrounding the abundant endosperm whose cells are full of oil droplets. The embryo is 3–4 mm long, situated apically near the micropyle, and has two flat, erect cotyledons.

Carpels of various species differ somewhat in size and also color and sculpturing of the endocarp. In three Mauritian species belonging to Group 5 (i.e., *Tambourissa amplifolia, T. pedicellata,* and *T. tau*), it has sparsely branched, longitudinal ridges. Otherwise the carpels provide few taxonomically useful characters. Birds appear to be the effective seed vectors in *Tambourissa* (D. Lorence, pers. observ.; A. Rolland, pers. comm.; *Benson 142,* BM).

In summary, morphological and anatomical features of the wood, stems and phyllotaxy, leaves, inflorescence, flowers, and fruits of the Malagasy Monimiaceae often display marked trends and provide important diagnostic characters at the generic level. Furthermore, features of trichomes, inflorescence, and in particular floral morphology and anatomy also provide valuable diagnostic features at the specific level.

POLLEN

As a detailed palynological study of the Malagasy Monimiaceae has been published elsewhere (Lorence et al., 1984), only a brief summary of the results will be given here.

The four genera studied here all possess inaperturate spheroid, subspheroid, or ovoid pollen characteristic of the majority of the Monimiaceae sensu stricto excluding the Atherospermoideae, whose pollen is disulcate (Money et al., 1950; Walker, 1976). Although Walker (1976) probably meant to exclude the spinose pollen of *Monimia* (Monimioideae), his statement that pollen of ". . . most of the genera on Madagascar and the Mascarenes is distinctive in possessing spiral bands on the surface" in the manner of *Hortonia* (Hortonioideae; Ceylon) does not accurately describe the pollen of the other three genera (all Mollinedioideae). Their sexines exhibit variable patterns ranging from spinose in *Monimia,* corrugate in *Decarydendron,* either granulate, reticulate, striato-rugulate, striato-reticulate, or tectate in *Tambourissa* (including *Phanerogonocarpus*), to granulate with verrucate, gemmate, or even vesiculate processes in *Ephippiandra* (including *Hedycaryopsis*) (Lorence et al., 1984).

It was found that pollen size, exine thickness, and sexinous patterns appear to provide useful, species-specific characters in the majority of species examined in this study. Although palynological evidence does not support the segregation of *Hedycaryopsis* from *Ephippiandra,* nor of *Phanerogonocarpus* from *Tambourissa,* generic differences in pollen are otherwise distinctive.

CHROMOSOME NUMBERS

As chromosome numbers provide some degree of support for the segregation of at least some of the subfamilies of Monimiaceae (e.g., Ehrendorfer et al., 1968; Goldblatt, 1974), and because all of the genera in the Malagasy region were previously unknown cytologically, it was decided to accumulate as much chromosomal information as possible during this study. All the reported counts were obtained from androecious flower buds fixed in 3 : 1 absolute ethanol : glacial acetic acid and later examined by the acetocarmine squash method.

Chromosomal study of all three species of *Monimia* has proven extremely difficult because of their small size and high number, a difficulty compounded by their tendency to stick together and by the presence of cytoplasmic inclusions. As a result, only approximate counts were obtained, both for *Monimia rotundifolia*: Réunion, Bébour cloud forest, *Lorence 2429* (MO), $n =$ ca. 44; Réunion, Col de Bellevue, cloud forest, *Lorence 2473* (MO), $n =$ ca. 48. The gametic chromosome number for this species therefore lies somewhere between 40 and 50, and it is obviously paleopolyploid.

These chromosomal findings for *Monimia* do not appear to suggest any close numerical affinity with *Peumus* ($2n = 78$; Morawetz, 1981). Both genera appear to be polyploids, however, as opposed to the majority of Monimiaceae sensu stricto (P. Goldblatt, pers. comm.).

All nine species of *Tambourissa* examined cytologically in this investigation had a gametic chromosome number of $n = 19$ (Table 9).

Although six of the species were from Mauritius, a few from Grande Comore, Réunion, and Madagascar were also examined with the same results. This suggests that the extensive adaptive radiation of *Tambourissa* in the Malagasy region has occurred at the same chromosomal level.

The paleohexaploid base number $x = 19$ (Goldblatt, 1980) is shared with a number of genera from Oceania also belonging to Mollinedioideae sensu Thorne (1974)—i.e., *Hedycarya, Levieria, Palmeria,* and *Wilkiea* (Ehrendorfer et al., 1968)—as well as by *Hortonia* in the Hortonioideae (Goldblatt, 1974). As in *Tambourissa,* these genera are characterized by androecious flowers bearing numerous, irregularly spaced subsessile stamens with lateral dehiscence (Ehrendorfer et al., 1968), although gynoecious floral construction is more variable (Endress, 1980b). Similarities in cytology and androecious floral morphology among these genera suggest they are relatively closely allied within the Mollinedioideae.

The remaining endemic Madagascan genera belonging to the Mollinedioideae—i.e., *Decarydendron* and *Ephippiandra* (including *Hedycaryopsis*) as well as both *Tambourissa* species formerly included in *Phanerogonocarpus*—are unknown cytologically.

Floral Biology

Although the vegetative and floral anatomy (Money et al., 1950), palynology (Walker, 1976), and cytology (Ehrendorfer et al., 1968; Goldblatt, 1974) of various extant primitive angiosperm families have been relatively well studied, comparatively little is known of their floral biology and breeding systems. I have therefore attempted to accumulate as much data as possible on these aspects of the Monimiaceae while in the Malagasy area.

The only confirmed report on pollination in Monimiaceae sensu stricto is by Gottsberger (1977), who observed female thrips making holes and ovipositing in androecious and gynoecious flower buds of *Mollinedia* in Brazil. The larvae develop and mature inside the buds and the adults emerge as the buds open, flying out and carrying pollen to other flowers as they seek mates. Endress (1979, 1980b) also reported finding holes and eggs in flowers of *Wilkiea* and *Stegnanthera* (Mollinedioideae), which may have been from pollinating insects. More recently, investigations by Thien (1980) on the pollination of species of primitive angiosperms belonging to the Degeneriaceae (*Degeneria*) and Winteraceae (*Drimys, Belliolum,* and *Zygogynum*) in the South Pacific islands show that members of the orders Coleoptera, Diptera, Lepidoptera, and Thysanoptera are important pollinators of these plants.

The present study was conducted in Mauritius during 1978–1979 and includes observations on seven species of *Tambourissa* and one species of *Monimia.* The species studied, study sites, and observation periods are given in Tables 10 and 11. Insect visitors were captured, killed, and mounted or stored in 70% alcohol for identification. Flowers of all species studied were observed and photographed during various stages. Voucher specimens of the plants are deposited at MAU and MO.

Tambourissa is a genus of monoecious or dioecious shrubs, treelets, or trees. All species have highly specialized, unisexual flowers with minute, scale-like tepals, a well-developed receptacle which assumes the functions of a perianth and ovary wall, and inferior carpels. As an understanding of the floral morphology is essential to understand the pollination biology, this chapter should be read in conjunction with the section on floral morphology and anatomy.

Female receptacles of most species are somewhat globose and closed in bud, and split open at maturity into (3–)4–5(–10) lobes, depending on the species. Once open, they do not close again. The receptacle is lined with numerous short to long styles, each corresponding to a single carpel. These become receptive gradually and centripetally during floral anthesis, which typically lasts 10–15 days. Receptive styles of most species produce a slight mucilaginous exudate in which the pollen tubes germinate and grow (e.g., *Tambourissa tau, T. cordifolia,* Figs. 13E, 16C). In others, the styles are reduced and covered by a massive mucilaginous secretion (compitum) (e.g., *T. peltata,* Fig. 17E). In yet others (e.g., *T. purpurea*), the flower remains closed except for a mucilaginous plug which occludes the floral entrance and has a stigmatic function (Endress,

TABLE 9. Collections of *Tambourissa* in which the haploid chromosome number was determined as $n = 19$. All collections are mine; vouchers are deposited at MO and most at MAU also.

Species	*Lorence* Number	Locality
T. comorensis	*2878*	Grande Comore. La Grille, wet forest.
T. cordifolia	*2571*	Mauritius. Pétrin Nature Reserve, *Philippia* heath formation.
T. elliptica		
subsp. *elliptica*	*2526, 2530*	Réunion. Takamaka, wet forest.
subsp. *micrantha*	*2483*	Réunion. Mare Longue, wet forest.
T. pedicellata	*2384*	Mauritius. Pieter Both Mt., degraded wet forest.
T. peltata	*2553*	Mauritius. Cascade Alexandra, stunted wet forest.
T. purpurea	*1726*	Madagascar. Wild, locality unknown (cult. MO).
T. quadrifida	*2539*	Mauritius. Matala Valley (Yemen), semideciduous dry forest.
T. sieberi	*2250*	Mauritius. Mt. Cocotte Nature Reserve, cloud forest.
T. tau	*1964*	Mauritius. Piton de la Rivière Noire, wet forest.
T. tau	*2951*	Mauritius. Perrier Nature Reserve, wet forest.

1979, 1980b; as *T. religiosa*). This "hyperstigma" occurs in some Madagascan and Réunion species, but is absent from Mauritian and Comorean plants. The sweet mucilage of *T. purpurea* tested positive for reducing sugars with Benedict's solution and for glucose with Lilly TES-tape (paper for analysis of urine sugar), respectively (Endress & Lorence, 1983). It therefore probably has a nectar function in a number of species that produce an abundant secretion (e.g., *T. crassa, T. elliptica, T. peltata, T. purpurea*). Flowers of most Mauritian species also produced strong floral odors which presumably attract pollinators.

Androecious flowers are similarly lined with numerous stamens that also mature gradually and centripetally after the globose receptacle splits into (3–)4–5(–7) subequal valvate segments. Although a few Comorean and Madagascan species open by a small apical orifice, lobes of most species open flat or even recurve and remain permanently open during their 7–12 day life span. Androecious flowers produce large amounts of pollen, which represent a substantial floral reward, although secretions are absent. In addition, floral odors like those in the gynoecious flowers are emitted.

In the Mauritian *Tambourissa* species, from one to more than 100 flowers were found to be open on a given day, depending on the species and individual, and flowering generally occurred over a three to five month period. These aspects will be discussed below in more detail by species. A synopsis of the results of this study for *Tambourissa* in Mauritius is as follows.

1. Major pollinators are insects belonging to the orders Coleoptera and Diptera.
2. Gynoecious floral morphology, notably size of the floral entrance, plays a key role in regulating insect entry.
3. Floral odor, and possibly also color, plays an important role in attracting pollinators.
4. Floral reward in the androecious flower is pollen. Gynoecious flowers of some species attract by deceit, while in others a mucilaginous exudate seems to have a nectar function.
5. Demography, phenology, and breeding systems are related to pollinator syndromes.

TAMBOURISSA SIEBERI

Tambourissa sieberi, a large, monoecious canopy tree 8–10 m tall, is known from only a few restricted areas of mature wet and cloud forest in Mauritius. It is scarce and occurs as scattered individuals in low population densities, e.g., at Macabé forest (Table 4), and at Mt. Cocotte where it was studied (Table 10). Hundreds of flowers (16–90 per inflorescence) are produced in unisexual pleiochasia and thyrses arising in large numbers from the trunk and major branches from December to February.

Gynoecious flowers are globose with a small apical pore only 2–3 mm diam. (Fig. 20A). Several hundred long styles which are coalescent into groups fill the receptacle, leaving only a small central cavity (Fig. 15E). The styles are moist at anthesis due to a slight surface exudate. Androecious flowers are relatively large and split into five spreading, reflexed lobes bearing ca. 100–

TABLE 10. Localities for pollination biology studies in Mauritius.

No.	Locality	Vegetation Type	Elevation (m)	Annual Pptn. (mm)	Date	Season
1.	Mt. Cocotte	cloud forest	760	5,000	Jan. 1979	wet
2.	Matala valley (Yemen)	semideciduous dry forest	200	1,600	June–July 1979	dry
3.	Perrier	*Sideroxylon* lower montane wet forest	600	3,400	Sept.–Oct. 1978	dry
					Sept. 1979	dry
					Apr. 1979	end wet
4.	Pétrin	*Philippia* heath formation	630	4,000	May 1979	start dry
5.	Bel Ombre	Lowland wet (high) forest	300	2,400	Dec. 1978–Jan. 1979	wet
6.	Mare Longue Plateau	Lower montane wet forest	660	3,400	Apr. 1979	end wet
7.	Piton Brise Fer	Lower montane wet forest	700	2,400	Dec. 1978	wet

140 large stamens that release abundant, coalescent pollen. Flowers may be either pale yellow or dark reddish purple, depending on the individual. Flowers of both sexes produce the same strong, cloying odor of overripe or fermenting fruit.

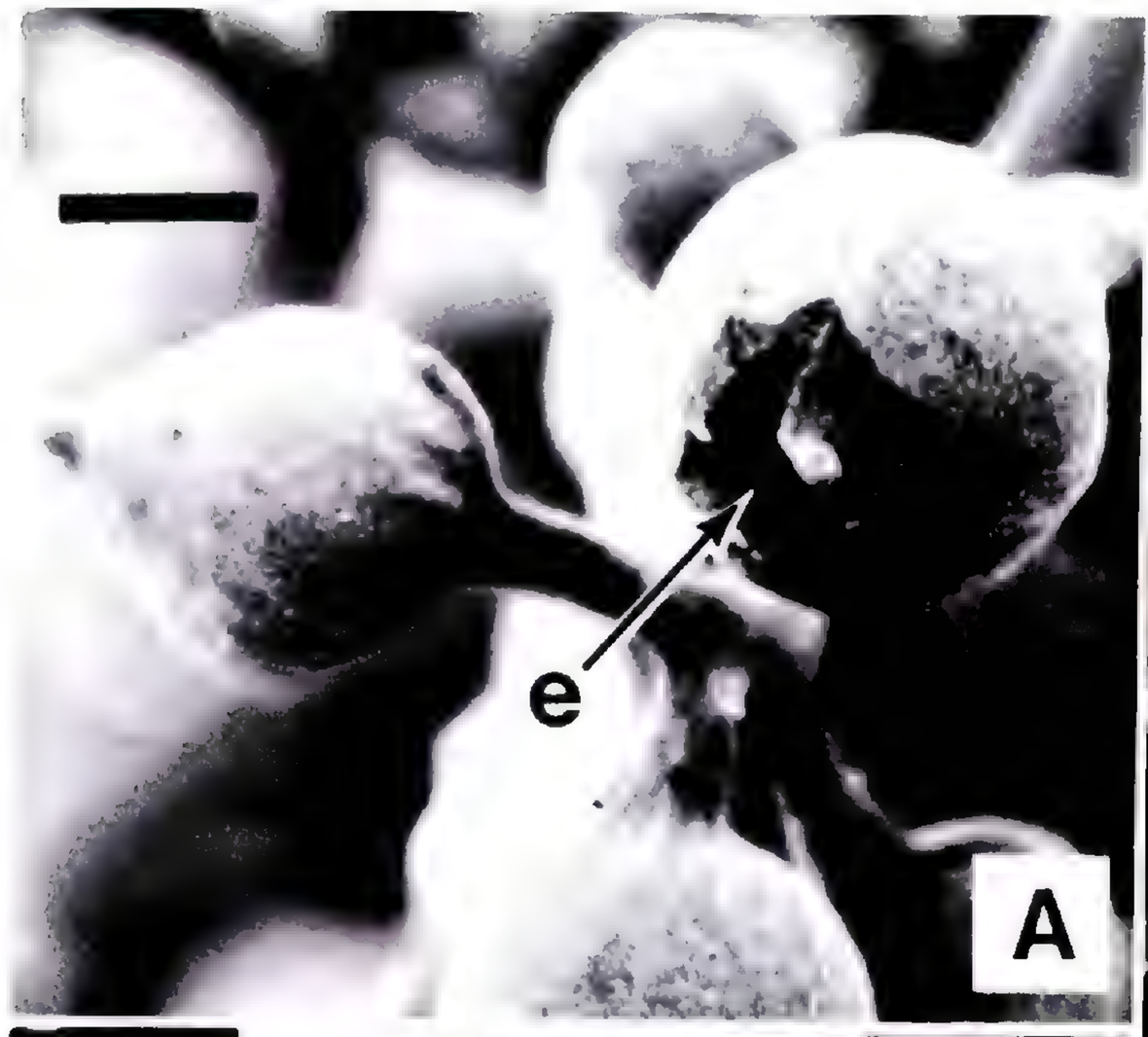
Observations made near midday, totalling 3.4 hours, revealed that introduced honeybees (*Apis mellifera*) were the most frequent visitors of androecious flowers, from which they gathered pollen. They showed no interest in the gynoecious flowers, however, nor could they enter them. Other less frequent visitors to the androecious flowers were unidentified Syrphidae (two species) and another unidentified dipteran (Table 11). No visitors were observed on the gynoecious flowers during this time, and no observations were made at night.

Examination of the contents of ten gynoecious flowers from the tree and 15 fallen flowers revealed the presence of various small arthropods, notably a variety of small Coleoptera only 2–3 mm long, in over half the flowers (Table 12). These Coleoptera, belonging to the families Hydrophilidae, Nitidulidae, Rhizophagidae, and Staphylinidae, are presumably active at night. They probably visit androecious flowers to feed on the pollen, attracted by the strong floral odors. They also enter the gynoecious flowers to feed on the styles, which were damaged in certain flowers, and probably oviposit there, as eggs and larvae were found in some flowers (Table 12). Because the stylar canal is situated near the style's base, damage to its terminal portion probably has little if any effect on pollen tube germination and growth which may occur anywhere on the stylar surface. Reduction of the floral entrance can be viewed as a strategy to protect the ovules from damage by larger, more destructive beetles (cf. Gottsberger, 1974, 1977; Endress, 1980b), at the same time allowing access to the less destructive small beetles. Elongation and coalescence of the styles may provide food for the coleopterans and also protect the ovules. Carpel group formation of this type, by connivence of the styles and cohesion by the mucilaginous secretion, functionally divides the gynoecium into several subunits, each being composed of a number of carpels (Endress & Lorence, 1983). This phenomenon is unknown elsewhere among the angiosperms.

Breeding experiments suggest that *Tambourissa sieberi* is the only self-compatible monoecious species of the four tested in Mauritius (Table 13). I suspect self-compatibility in *T. sieberi* may be a strategy to offset its low population densities and probable inefficiency of the small pollinators. Production of a large number of flowers and a prolonged flowering period may also compensate for these factors.

TAMBOURISSA QUADRIFIDA

Tambourissa quadrifida is the only species of Monimiaceae to occur in the dry forest zone of Mauritius. A mid stratum or subcanopy tree, it occurs in small, scattered populations and readily forms multiple coppice stems. Individuals are subdioecious, producing flowers of predominantly one sex, and flower from June to August. The numerous flowers are produced in pleiochasia and thyrses along the trunk, and hundreds of flowers may be open on a given day, each persisting for ca. 10–15 days. During the 1979 flowering season, a predominantly androecious tree (*Lorence 2656,* MO) was estimated to produce nearly 24,000 flowers, and a predominantly gyn-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oecious tree (*Lorence 2655,* MO) over 15,000 flowers! Crossing experiments carried out on three individuals showed them all to be self-incompatible (Table 13).

The gynoecious flowers of *Tambourissa quadrifida* are ellipsoid to obovoid and open by a small apical pore only 1–2 mm diam. (Fig. 20B). Inside, 200–300 short, glistening pink or yellow styles line the hollow receptacle; only a small amount of stylar exudate is produced. The orange or red androecious flowers split into four ultimately recurved segments bearing 300–500 stamens with slightly coalescent pollen (Fig. 20B). A strong, pleasant odor of ripe fruit is produced by flowers of both sexes.

Studies were carried out on a population of four individuals at Yemen (Matala Valley) on the edge of a dry forest degraded by numerous exotics. Observations totalling 13.4 hours revealed that large numbers of small Diptera (*Drosophila* spp., *Homoneura,* and *Zaprionus*) congregated on the androecious flowers in the early morning, but did not enter the gynoecious flowers (Table 11). For this reason, the drosophilids presumably have little, if any, effect as pollinators. Three species of syrphids also visited the androecious flowers occasionally during the day to feed on the pollen, and pollen foraging activity by honeybees was also intense throughout the day. As these insects are all too large to enter the gynoecious flowers in which the styles are concealed, they cannot function as pollinators.

An examination of 438 gynoecious flowers from the tree and 132 fallen flowers revealed that 93.6% and 75.8% respectively were devoid of any contents (Table 14). A number contained mealybugs which were presumably brought in by the small ants also found in some flowers. Ants are probably ineffective as pollinators, as they did not visit androecious flowers. A small percentage of flowers contained silk webbing, often with small larvae or pupae (probably Lepidoptera). These larvae appeared to graze on the styles and probably represent predators, although pollinating activity by the ovipositing adults cannot be discounted. The only likely pollinator observed was a small Nitidulidae beetle, *Haptoncus luteolus* (Tables 11, 14) seen emerging from a gynoecious flower. It subsequently visited an androecious flower to forage for pollen, which adhered to its body. The beetle is probably able to travel the short distances of several meters separating trees in this population. Significantly, another species of *Haptoncus* was seen in the structurally similar gynoecious flowers of *Tambourissa sieberi* (Table 12), and Thien (1980) found the same genus in *Degeneria* flowers.

One factor responsible for the scarcity of pollinators on *Tambourissa quadrifida* at Yemen may have been the disturbed, partly secondary nature of the habitat. However, the predominantly gynoecious tree of the four usually produces some fruit clusters each year (J. A. Lalouette, pers. comm.), indicating that effective cross pollination does occur to a certain degree.

As in *Tambourissa sieberi,* an extreme reduction of the gynoecious floral entrance excludes larger, more destructive insects, permitting only smaller pollinators like the nitidulid to enter. The tremendous floral production in *T. quadrifida* presumably offsets the lower efficiency of these insects as pollinators as in *T. sieberi,* whereas self-incompatibility and subdioecy would enforce outcrossing.

TAMBOURISSA TAU

Tambourissa tau is a slender, monoecious understory treelet rarely exceeding 2–3 m high. Flowers are produced from meristematic swellings along the main stem, or in the leaf axils. Depending on its size, each plant may produce over 100 solitary or fasciculate flowers over a three to five month period, but only several open at a time, each lasting for 10–15 days. Crossing experiments revealed it to be self-sterile (Table 13).

Gynoecious flowers are relatively small, externally corky, and split about half way open into 6–10 irregular, suberect lobes (Fig. 39E, F). Each

←

FIGURE 20. Flowers of some *Tambourissa* species.—A. *T. sieberi,* gynoecious flowers in bud (left) and at anthesis (right), note insect egg (e) in orifice, *Lorence 2250* (MO).—B. *T. quadrifida,* inflorescences with gynoecious flowers (left), note small orifice (o), and androecious flowers (right), *Lorence 2656* (MO).—C. *T. cordifolia,* androecious plant with flowers in bud and at anthesis, note visiting drosophilids (d), *Lorence 2632* (MO).—D. *T. crassa,* gynoecious flower at anthesis, note visiting dipteran (d) drinking mucilage, *Lorence 2468* (MO).—E. *T. ficus,* form with partly closed white androecious flowers in bud, at anthesis and post anthesis, *Lorence 1485* (MO).—F. *T. ficus,* form with open purple androecious flower at anthesis, note visiting syrphid (s), *Lorence 2115* (MO). Bars equal 10 mm.

TABLE 11. Pollination biological data for species of Monimiaceae in Mauritius.

Species	Loc.	Date	Time	Weather	T° (C)	Total Obs. Time (hr.)	Insect Visitors/Pollinators	Max. Obs.	No. Flowers Observed
Monimia ovalifolia	1	10 Aug. 1979	11:30 A.M.–1:40 P.M.	cloudy, rainy	16–17.5	2.2	Diptera Syrphidae cf. *Isciodon* sp.	5	numerous
Tambourissa amplifolia	5	10 Jan. 1979	9:10 A.M.–1:40 P.M.	sunny to rainy	26–30	4.5	Diptera Drosophilidae *Drosophila* cf. *nasuta* Lauxaniidae *Homoneura* sp.	1 3	6 ♀, 18 ♂ 6 ♀, 18 ♂
T. cordifolia	4	12 May 1979	1:20 P.M.–5:30 P.M.	sunny to rainy	26–22	4.2	none	0	9 ♂
	4	13 May 1979	6:30 A.M.–11:30 A.M.	dawn to sunny & windy	18–26.5	5.0	Diptera Drosophilidae *Drosophila nasuta* *Zaprionus vittager*	total 72	9 ♂ 9 ♂
	4	13 May 1979	6:45 A.M.–11:10 A.M.	dawn to sunny & windy	18–26.5	4.4	Diptera Drosophilidae *Drosophila nasuta* Lauxaniidae *Pachycerina* sp.	total 12	6 ♀ 6 ♀
	4	19 May 1979	5:00 P.M.–6:45 P.M.	sunny & windy to dusk	19.5–16	1.8	Diptera Drosophilidae *Drosophila nasuta*	1	7 ♂
	4	30 May 1979	6:05 A.M.–9:05 A.M.	dawn to sunny & windy	18–26	3.0	Diptera Drosophilidae *Zaprionus vittager* Lauxaniidae *Homoneura* sp.	total 12	6 ♂ 6 ♂
	4	30 May 1979	6:45 A.M.–11:15 A.M.	dawn to sunny & windy	19–26	4.5	Diptera Drosophilidae *Drosophila nasuta*	1	6 ♀

TABLE 11. Continued.

Species	Loc.	Date	Time	Weather	T° (C)	Total Obs. Time (hr.)	Insect Visitors/Pollinators	Max. Obs.	No. Flowers Observed
Tambourissa ficus	7	8 Dec. 1978	11:00 A.M.–11:50 A.M.	fair	23.5–25	0.8	Diptera		
							Syrphidae		
							Eumerus sp.	2	2 ♂
	1	12 Dec. 1978	8:45 A.M.	fair	—	spot check	Coleoptera		
							Hydrophilidae		
							Cercyon sp.	42	2 ♀, 1 ♂
T. peltata	6	10 Apr. 1979	7:30 A.M.–11:30 A.M.	fair & occ. rain	20–27	4.0	Diptera		
							Drosophilidae (unidentified)	4	16 ♀
							Syrphidae		
							cf. *Askarina*	1	16 ♀
							Diptera (unidentified)	1	16 ♀
	6	19 Apr. 1979	3:45 P.M.–5:30 P.M.	fair, sunny	25–21	1.8	Diptera		
							Syrphidae (unidentified)	1	12 ♀
	3	9 Apr. 1979	10:30 A.M.–10:50 A.M.	fair	24–25	0.3	Diptera		
							Syrphidae		
							Askarina sp.	3	6 ♂
							Hymenoptera		
							Apidae		
							Apis mellifera	1	6 ♂
	3	9 May 1979	11:00 A.M.–11:20 A.M.	fair	25	0.3	Diptera (small, unidentified)	3	2 ♀
	3	10 May 1979	3:45 P.M.–4:00 P.M.	fair	28.5–27	0.3	Diptera (small, unidentified)	1	2 ♀
	3	11 May 1979	3:20 P.M.–4:00 P.M.	fair	28–24.5	0.7	Hymenoptera		
							Apidae		
							Apis mellifera	3	8 ♂
	3	12 May 1979	8:15 A.M.–9:00 A.M.	passing showers	22–23	0.8	Diptera		
							Drosophilidae		
							Drosophila (*melanogaster* grp.)	many	25 ♂
							D. nasuta	many	25 ♂
							Zaprionus hibernaculatus	many	25 ♂
							Syrphidae		
							Askarina sp.	1	25 ♂
							Ornida obesa	2	25 ♂

TABLE 11. Continued.

Species	Loc.	Date	Time	Weather	T° (C)	Total Obs. Time (hr.)	Insect Visitors/Pollinators	Max. Obs.	No. Flowers Observed
Tambourissa quadrifida	2	20 June 1979	7:12 A.M.–11:40 A.M.	fair to cloudy	20–24.5	4.5	Diptera		
							Drosophilidae		
							Drosophila sp.	several	hundreds ♂
							Zaprionus sp.	1	hundreds ♂
							Syrphidae		
							Ornida obesa	1	hundreds ♂
							Hymenoptera		
							Apidae		
							Apis mellifera	5	hundreds ♂
	2	21 June 1979	7:20 A.M.–11:45 A.M.	fair to cloudy	20–24	4.4	Diptera		
							Lauxaniidae (unidentified)	1	several ♂
							Syrphidae (unidentified)	1	several ♂
	2	22 June 1979	7:00 A.M.–11:30 A.M.	fair to cloudy	19.5–24	4.5	Diptera		
							Drosophilidae		
							Drosophila nasuta	many	hundreds ♂
							D. (*melanogaster* grp.)	many	hundreds ♂
							Zaprionus sp.	2	hundreds ♂
							Lauxaniidae		
							Homoneura quadrivittata	3	hundreds ♂
							Syrphidae (2 spp., unident.)	3	hundreds ♂
							Coleoptera		
							Nitidulidae		
							Haptoncus luteolus	1	1 ♀
							Hymenoptera		
							Apidae		
							Apis mellifera	6	hundreds ♂
T. sieberi	1	4 Jan. 1979	11:00 A.M.–12:12 P.M.	fair to cloudy	28–29	1.2	Hymenoptera		
							Apidae		
							Apis mellifera	6	many ♂

TABLE 11. Continued.

Species	Loc.	Date	Time	Weather	T° (C)	Total Obs. Time (hr.)	Insect Visitors/Pollinators	Max. Obs.	No. Flowers Observed
	1	4 Jan. 1979	12.45 P.M.–1:55 P.M.	fair to cloudy	25.5–24	1.2	Diptera		
							Syrphidae (unidentif.)	3	many ♂
							Diptera (unidentified)	1	many ♂
	1	17 Jan. 1979	1:10 P.M.–2:10 P.M.	cloudy	27–23.5	1.0			
							Diptera		
							Syrphidae (unidentified)	2	many ♂
							Diptera (unidentified)	1	many ♂
							Hymenoptera		
							Apidae		
							Apis mellifera	1	many ♂
T. tau	3	8 Oct. 1978	3:30 P.M.–5:30 P.M.	fair to rainy	23.5–22	2.0	Coleoptera		
							Curculionidae		
							Scaevinus truncatus	1	4 ♂
	3	17 Oct. 1978	3:00 P.M.–4:20 P.M.	fair	23–22	1.3	*Scaevinus truncatus*	2	1 ♂
	3	18 Oct. 1978	9:30 A.M.–11:00 A.M.	fair	19.5–22.5	1.5	Coleoptera		
							Curculionidae		
							Scaevinus truncatus	2	3 ♂
	3	20 Oct. 1978	—	fair	—	spot check	*Scaevinus truncatus*	1	1 ♂
	3	23 Oct. 1978	2:30 P.M.–3:00 P.M.	fair	25–24	0.5	*Scaevinus truncatus*	2	2 ♂
	3	6 Dec. 1978	—	—	—	spot check	*Scaevinus truncatus*	1	1 ♂
	3	2 Sept. 1979	6:00 A.M.–11:30 A.M.	fair to rainy	17–23	5.5	*Scaevinus truncatus*	1 (on ♀)	4 ♀, 4 ♂

TABLE 12. Contents of *Tambourissa sieberi* gynoecious flowers sampled at Mt. Cocotte, Mauritius in January 1979.

Contents	No. Flowers From Tree	% Total	No. Flowers From Ground	% Total
Empty	10	45.5	15	41.7
Small Coleoptera: (Hydrophilidae, *Dactylosternum vinsoni* B.B.; Nitidulidae, *Carpophilus mutilatus* Er., *Epuraea terminata* Rtt.,[a] *Haptoncus minutus* Rtt., *Lasiodactylus pictus* MacL.; Rhizophagidae, *Europs* cf. *brevis* Gronv.; Staphylinidae, *Atheta dilutipennis* Mots., *Philonthus flavocinctus* Mots.	6	27.3	13	36.1
Lepidoptera (*Opogona sacchari* Bojer, larva, presumably a predator)	1	4.5	5	13.9
Unidentified larvae (possibly Diptera)	2	9.1	0	0
Ants (Hymenoptera, Formicidae)	0	0	1	2.8
Isopod	2	9.1	0	0
Unidentified insect eggs	1	4.5	2	5.5
Total	22	100.0	36	100.0

[a] Three individuals of *Epuraea terminata* also found on bagged androecious flowers of *T. sieberi* at this site.

flower contains 80–100 long, dark purple-red setose styles which secrete a slight mucilaginous exudate on the surface (Fig. 16C). Androecious flowers split into 5–7 irregular, flat lobes and contain 100–150 T-shaped stamens with loculi held on lateral arms (Figs. 18H, 39B, C). The pollen is only slightly cohesive. Androecious flower color may be either dark purple-red or greenish white internally. I was unable to detect any floral odor from *T. tau* flowers during either day or night.

A population of *Tambourissa tau* at Perrier Nature Reserve was observed for pollinators for a total of 10.8 hours. The only insect to visit the flowers with any regularity was *Scaevinus truncatus*, a cryptic, nocturnal folivorous weevil found to occur on most species of *Monimia* and *Tambourissa* in Mauritius and Réunion. *Scaevinus* normally feeds on the leaves of *T. tau*, but during the flowering season weevils were found feeding on buds and flowers, grazing on the stamens, styles, and receptacle lobes. Large numbers of pollen grains were found trapped among the insects' body hairs and scales. To test the weevil's vagility, marking experiments were carried out on *Scaevinus* at Perrier. Among 52 individuals of *T. tau* studied, 8–28% were found to harbor *Scaevinus* on a given day. Out of 27 *Scaevinus* marked at the onset of the experiment, 18 (67%) had moved to other plants in the same population after three days. As *T. tau* occurs at comparatively high population densities at Perrier (57 plants/512 m², or an estimated 1,113/ha), with nearest neighbor distances averaging only 160 cm (Fig. 3B), and fruit set in the wild is relatively high, it appears that *Scaevinus* is effective in cross pollinating *T. tau*. Although *Scaevinus* was also seen feeding on flower buds of *T. peltata* at Perrier, it was never observed to visit its flowers, nor those of any other *Tambourissa* or *Monimia* species. Finally, no other insects were observed to visit the flowers of *T. tau*.

TAMBOURISSA CORDIFOLIA

A study of this species was carried out at Pétrin Nature Reserve where *Tambourissa cordifolia* is common and forms dense, local populations in a low, scrubby *Philippia* heath formation. It is a small, dioecious shrub 1–2 m high with erect, multiple stems bearing medium-sized solitary or fasciculate flowers on leafless nodes. The androecious flower splits into four flat, spreading-reflexed lobes with 300–400 white stamens (Figs. 20C, 42B), which release white, coalescent pollen. The hollow, obconic gynoecious receptacle is shallow and splits apically into four erect or outcurved deltoid lobes that are ribbed and whitish within (Fig. 42G, H). The floral entrance is 10–12 mm wide and allows access to 100–400 short, purple-red conical styles that produce a sparse surface secretion (Fig. 13E). Flowers of both sexes emit a strong, pleasantly fruity floral odor likened by various observers to that of ripe

TABLE 13. Summary of results of *Tambourissa* crosses carried out in Mauritius (1978–1979) and at the Missouri Botanical Garden (1980).

Species & Locality	No. ♀ Flowers Outcrossed	No. Fruits Developed	% Fruit Set	No. ♀ Flowers Selfed	No. Fruits Developed	% Fruit Set
T. amplifolia, Bel Ombre	8 (3 individuals)	1	12.5	8 (3 individuals)	0	0
T. cordifolia, Pétrin	4 (2 individuals)	3	75.0	(Dioecious)	—	—
T. cordifolia × *T. peltata*,	8 (2 individuals)	1	12.5	—	—	—
T. peltata, Perrier	7 (2 individuals)	7	100.0	(Dioecious)	—	—
T. peltata × *T. cordifolia*	2 (1 individual)	2	100.0	—	—	—
T. purpurea, cultivated, St. Louis	—	—	—	15 (1 individual)	0	0
T. quadrifida, Yemen Valley	15 (3 individuals)	14	93.3	16 (3 individuals)	0	0
T. sieberi, Mt. Cocotte	2 (2 individuals)	2	100.0	11 (2 individuals)	4	36.4
T. sieberi × *T. tau*	2 (1 individual)	2	100.0	—	—	—
T. tau, Perrier	12 (8 individuals)	12	100.0	16 (8 individuals)	0	0

apricots, ripe stewed bananas, or ripe jackfruit, which is perceptible for several meters. The species is dioecious and therefore obligately outcrossing.

A mature flowering individual of each sex was selected for study totalling 23 hours of observation time (Table 11). Pollinator activity began at dawn (ca. 5:45 A.M.) as the dense mists dispersed. Numerous small dipterans then began congregating on both androecious and gynoecious flowers (up to 25 insects per flower; Fig. 20C) drawn by the strong, fruity odor. *Drosophila nasuta* and *Zaprionus vittiger* were the most frequent visitors, with smaller numbers of *Lyciella* and *Homoneura* (both Lauxaniidae) (Table 11). The insects fed on the pollen of the androecious flowers and drank dew and possibly stylar exudate from the gynoecious flowers. Considerable interfloral and interplant movement occurred at this time. Insect activity began to abate after 7:00–8:00 A.M. with an increase in temperature and wind velocity and generally ceased completely by 9:00 or 10:00 A.M.

Pollen grains adhered to the bodies of all the insects examined, suggesting they are effective as pollen vectors, although no actual pollen counts were made. In addition, the population density of *Tambourissa cordifolia* was extremely high at Pétrin (69 individuals/410 m^2, or an estimated 1,684/ha), with a mean nearest neighbor distance of 78.5 cm (Fig. 3C). Over 50% of the individuals in this population were actually situated within 50 cm of each other (Fig. 3C).

Judging by the relatively high wild fruit set and good regeneration of *Tambourissa cordifolia* at Pétrin, ample cross pollination takes place. As Drosophilidae breed in decaying fruit and fungi, and Lauxaniidae breed in decaying vegetation (Borror & Delong, 1971), it is likely that significant pools of these insects are available during the plants' three to five month flowering period. Significantly, Thien (1980) also recorded two of the same dipteran genera (*Drosophila* and *Homoneura*) as pollinators of *Drimys* in New Guinea.

TAMBOURISSA AMPLIFOLIA

A slender treelet 6–8 m tall, *Tambourissa amplifolia* is occasional to locally common in the understory of some lowland and lower montane wet forest areas in Mauritius. It is monoecious and basally cauliflorous. Flowering takes place from November through January and up to 24 long-pedicellate flowers are open at a given time, each lasting for 10–15 days.

The white androecious flowers split into four flat lobes and resemble those of *Tambourissa cordifolia*, but are only half as large with 150–200 stamens (Fig. 18B). The shallowly napiform gynoecious flowers also resemble those of *T. cordifolia*, but are half as large with four everted lobes, a broad orifice, and ca. 300 short, yellow or purple styles situated in the shallow, discoid receptacle. Only slight amounts of mucilage are secreted by the styles. Flowers of both sexes produce a faint, fruity odor.

One individual of *Tambourissa amplifolia* was observed at Bel Ombre for a total of 4.5 hours during the morning (Table 11). Several drosophilids (*Drosophila* cf. *nasuta* and *Homoneura* sp.) repeatedly visited flowers of both sexes. Al-

TABLE 14. Contents of *Tambourissa quadrifida* gynoecious flowers sampled at Matala Valley (Yemen), Mauritius in March, June, and July 1979.

Contents	No. Flowers From Tree	% Total	No. Flowers Fallen From Ground	% Total
Empty	410	93.6	100	75.8
Mealybugs (Homoptera, probably Pseudoccidae)	1	0.2	15	11.4
Ants (Hymenoptera, Formicidae)	14	3.2	4	3.0
Silk webbing & pupa (probably Lepidoptera)	6	1.4	3	2.3
Silk webbing & larva (probably Lepidoptera)	2	0.5	2	1.5
Coleoptera, Nitidulidae, *Haptoncus luteolus*	1	0.2	—	—
Detritus (feces)	3	0.7	5	3.8
Empty egg cases	1	0.2	2	1.5
Springtail (Collembola)	—	—	1	0.7
Total	438	100.0	132	100.0

though visits were less extensive than in *T. cordifolia,* the same pollinator syndrome appears to be operative. Individuals of *T. amplifolia* are generally separated by distances less than 10 m, which the insects should be able to cross. Outcrossed flowers of *T. amplifolia* yielded a low fruit set (12.5%) although it is unclear why (Table 13).

TAMBOURISSA PELTATA

A medium-sized dioecious canopy tree, *Tambourissa peltata* is common and widespread in wet and cloud forests throughout the island. Flowering lasts from March to June and each individual generally has three to ten flowers open at a given time, although a large androecious plant may produce up to 58 open flowers during peak flowering. The exposed flowers are produced either singly or in groups of two to three on the older, leafless branches in the canopy and on the upper trunk, thus making pollination studies difficult. It is dioecious and obligately outcrossing.

The broad gynoecious receptacle splits open by four or five ornate, dark purple-red verrucose sterile lobes that spread flat, resembling a *Stapelia* flower (Figs. 15A, 17E). The flat gynoecial disc is orange and bears ca. 400–500 flat, densely crowded columnar styles. At anthesis, the entire disc is covered by a layer of thick, sweet mucilage that functions both as a compitum and as nectar. Androecious flowers split gradually into four or five ultimately reflexed lobes bearing 200–400 stamens that release abundant, coalescent pollen (Fig. 17D). Both salmon pink and dark purple-red androecious color morphs occur, according to the individual. Flowers of both sexes produce a strong, sour odor of rotting fruit or tomatoes and persist on the tree for 10–15 days.

The species was studied at Mare Longue Plateau and at Perrier and Pétrin Nature Reserves (Table 11) for a total of 8.2 hours and supplemented by additional insect collections. Most frequent visitors were Diptera, notably Syrphidae and Drosophilidae (Table 11). In the early morning, large numbers of *Drosophila* and *Zaprionus* congregated on both androecious and gynoecious flowers as in *Tambourissa cordifolia,* in addition to a few small Coleoptera (*Enicmosoma, Epuraea*). As the sun rose higher and the temperature increased, the drosophilids gradually left and were replaced by syrphids. The Syrphidae *Askarina* and *Ornida* were active throughout the day, periodically visiting different flowers on the same and on different trees. They often remained on flowers for extended periods to feed on the pollen (up to 43 minutes on a single flower for *Ornida obesa*), and also drank mucilage from the gynoecious flowers. Captured insects were found to have abundant pollen on their bodies. Other insect visitors included honeybees, which visited androecious flowers to gather pollen, but displayed no interest in the gynoecious flowers and their muciliage. The folivorous weevil, *Scaevinus truncatus,* while liv-

ing on *T. peltata* and feeding on its leaves and young flower buds, did not visit mature flowers and actually displayed an aversion to them, possibly repelled by the strong odor.

At Perrier, *Tambourissa peltata* occurred at comparatively low population densities of 26 individuals/12,700 m² (or an estimated 21/ha), with a mean nearest neighbor distance of 975 cm (Fig. 3A). Because of the relatively large distances separating individuals of this dioecious species, the strong-flying syrphids probably represent the most effective pollinators, although the role of drosophilids and small coleopterans as pollinators cannot be dismissed.

TAMBOURISSA FICUS

Tambourissa ficus is related to *T. peltata* but differs in being a small understory tree. It is usually subdioecious, producing one or two open flowers generally of a single sex at the swollen base of the trunk (Fig. 20E, F). Although only five to eight flowers are produced during the flowering season (Sept.–Dec.), they have the greatest dimensions of any in the family.

The urceolate-cupuliform gynoecious flower has a broad orifice and is lined with ca. 1,000–2,000 long, yellowish pink setose styles which secrete small amounts of mucilage (Fig. 15C). Two androecious floral forms occur, the first being cupuliform-urceolate like the gynoecious flower, with erect lobes and white stamens (Fig. 20E). The other form splits open flat into five to seven ultimately reflexed lobes with pinkish purple stamens (Fig. 20F). The thick, apiculate stamens number 900–1,800 in both forms. Flowers of both sexes emit a fetid-aminoid, but slightly fruity, odor.

A tree with flat purple androecious flowers at Brise Fer was observed for 0.8 hours at midday (Table 11). Male and female syrphids of the genus *Eumerus* were attracted to the flowers (Fig. 20F), and both captured insects had pollen adhering to their bodies. The cupuliform white androecious flowers on a tree at Rivière des Galets (Fig. 20E) were visited by a different dipteran (unidentified). At Mt. Cocotte, however, large numbers of small Hydrophilidae beetles of the genus *Cercyon* were found in gynoecious flowers and on open purple androecious flowers on a single tree. Significantly, members of the same family also visited gynoecious flowers of *Tambourissa sieberi* at the same locality, although their role in the pollination of *T. ficus* is uncertain.

Although no crosses were carried out for *Tambourissa ficus*, it is probably at least partly outcrossing because of its tendency towards dioecy. Scattered individuals as well as denser local populations occur, and syrphids would seem to represent the most efficient pollinators, although the Coleoptera may also play a role. More extensive observations on the pollination biology of *T. ficus* are obviously required.

Flowers of *Tambourissa crassa* (Réunion) emit a strong, rancid-fruity odor and appear to display the same pollination syndrome as *T. ficus*. A gynoecious individual of this dioecious species at Col de Bellevue (*Lorence 2468*, MO) was repeatedly visited by an unidentified dipteran which drank the mucilaginous secretion partly filling the mature gynoecious flower (Fig. 20D).

MONIMIA OVALIFOLIA

A low, dioecious tree restricted to small patches of cloud forest on the island's highest mountains, *Monimia ovalifolia* is the only member of the genus to occur in Mauritius. Its numerous small flowers are produced in ramiflorous inflorescences from August to November. The globose gynoecious receptacle takes on a pink to orange color at anthesis, but remains closed except for a small pore through which the six to 12 glistening white styles are exserted (Fig. 14B). These produce a slight surface secretion. The externally yellowish androecious flowers split into four or five recurved valvate segments (Fig. 14A) much like those of *Tambourissa*. The numerous white stamens possess paired basal appendages (as in Fig. 13A) and release coalescent pollen. Flowers of both sexes produce a strong, sweet odor.

Androecious and gynoecious trees of *Monimia ovalifolia* were observed for 2.2 hours at Mt. Cocotte (Table 11). The flowers appear to be myophilous and were repeatedly visited by small, unidentified Syrphidae that licked the styles and fed on the pollen. They were found to carry *Monimia* pollen and could probably traverse the relatively short distances separating individuals of *Monimia* at Mt. Cocotte. It is therefore likely that syrphids are effective pollinators of *Monimia ovalifolia* in Mauritius.

DISCUSSION

Tambourissa species in Mauritius exhibit two different modes of pollination involving Coleop-

tera and Diptera, modes that occur in a number of other extant primitive angiosperms (e.g., Faegri & van der Pijl, 1971; Gottsberger, 1974; Thien, 1980). Thrips, which are known to visit flowers of other primitive angiosperms including Monimiaceae (Gottsberger, 1977), were not found in this study, although it is possible that they may visit some of the small flowered Comorean and Madagascan species of *Tambourissa*.

Flowers of *Tambourissa quadrifida* and *T. sieberi* seem to be primarily cantharophilous with the fruity odors, dull colors, and numerous floral parts (i.e., stamens and styles) characteristic of this syndrome (e.g., Faegri & van der Pijl, 1971). The inferior ovaries and abundance of receptacular idioblasts (see Morphology and Anatomy section) are probably also protective in this context. Gynoecious flowers of both species are further adapted for pollination by a variety of small, probably allotropic, Coleoptera and differ from the classic Magnoliaceous cantharophilous flower in the following ways: the flowers are long lived, apetalous, and remain permanently open. Furthermore, the gynoecious floral entrance is small, thus excluding many destructive predators, although larvae of the indigenous moth, *Opogona sacchari,* successfully feed on flowers and developing fruits of at least three species, including *T. sieberi* (Table 11). Both species produce only traces of mucilage on their styles and presumably deceive the insects by their strong, ripe fruity odors, although the long styles of *T. sieberi* may also be utilized as food bodies. Androecious flowers of all *Tambourissa* species offer only pollen as a reward, a resource taken advantage of by a variety of Diptera and the introduced *Apis,* as well as by the effective pollinators. Mass flowering of these species may compensate for pollinator inefficiency.

The drab, apparently odorless flowers of *Tambourissa tau* seem to represent a specialized cantharophilous syndrome adapted to pollination by a single insect, the folivorous curculionid, *Scaevinus truncatus,* which feeds specifically on Monimiaceae leaves. The flowers of this species represent a supplementary food source for *Scaevinus,* and *T. tau* has taken advantage of its presence for use as a readily available pollinator. The long styles represent a food source for the insect, while the basal stylar secretions presumably trap pollen grains from its body and legs. The peculiar T-shaped stamens with widely separated loculi may maximize pollen contact with *Scaevinus,* while also rendering the pollen load less liable to be eaten at once. In any case, flowers of *T. tau* differ from the usual cantharophilous flowers and appear to be highly specialized. The energetic aspects of this relationship (cf. Heinrich & Raven, 1972) should prove to be most interesting.

The predominantly myophilous flowers of *Tambourissa amplifolia, T. cordifolia, T. ficus,* and *T. peltata* share a number of cantharophilous features with those of *T. quadrifida* and *T. sieberi,* i.e., strong fruity or aminoid odors and drab colors (in *T. ficus* and *T. peltata*). In fact, the latter two species also attracted some Coleoptera (Table 11), which is perhaps suggestive of a shift from cantharophily to myophily in *Tambourissa.* A number of other trends in these species suggest adaptations to allotropic fly pollinators (cf. Faegri & van der Pijl, 1971), including: paler floral colors (white androecious and pale yellow or pink gynoecious flowers in *T. cordifolia* and *T. amplifolia,* with white and salmon pink morphs occurring in androecious flowers of *T. ficus* and *T. peltata,* respectively), apically confluent anther loculi presenting the pollen more effectively (*T. amplifolia, T. cordifolia, T. peltata*); shallower and broader gynoecious receptacles with a larger entrance (extreme in the flat, discoid flowers of *T. peltata*), surrounded by attractive, spreading sterile lobes that act as landing platforms; more copious, sweet mucilaginous exudate with a nectar function in the gynoecious flower (*T. peltata,* Figs. 15A, 17E); a shortening of the stamens and styles to accommodate the insects' short probosces.

Although certain common features occur in these species, there appear to be two distinct trends. The first is a "fruit fly" syndrome involving small drosophilids that occurs in *Tambourissa amplifolia* and *T. cordifolia.* These plants are small in stature, occur in comparatively dense populations, and have smaller and paler flowers with a sweet, fruity odor produced near the ground. Significantly, Thien (1980) recorded two of the same fly genera as pollinators of *Drimys* in New Guinea, suggesting that these insects may pollinate a greater number of extant primitive angiosperms than previously suspected.

The second trend involves larger and more vigorous flies, primarily syrphids (in *Tambourissa ficus* and *T. peltata*). These are larger, more widely dispersed forest trees with more massive, pinkish to purplish flowers that emit sour, rancid, or otherwise fetid-aminoid odors with fruity overtones. Flowers are produced on the leafless upper branches (*T. peltata*) or near the ground

(*T. ficus*) and are exposed for easy access by the insects. Although androecious flowers of *T. ficus* were visited by syrphids and another dipteran in two cases (Table 11), flowers of both sexes of another individual attracted numerous hydrophilid beetles (*Cercyon* sp.). Hydrophilids were also found in gynoecious flowers of *T. sieberi* at this same site. A more thorough study of *T. ficus* is needed to detail its significant pollinators.

Monimia ovalifolia displays a number of myophilous features, namely, a sweet floral odor, yellow to pink or orange receptacles, shallow, permanently open white androecious flowers, well exposed stamens and styles. Its flowers are well adapted to the small, probably allotropic syrphids that visit them.

In summary, species of *Tambourissa* in Mauritius exhibit two different modes of pollination based on Coleoptera and Diptera, and each mode displays two distinct trends involving modifications in size, shape, color, and odor of the flower. Pollinator modes also appear to be related to demography and life forms. Pollinator specialization presumably contributes to reproductive isolation in simultaneously flowering sympatric species (e.g., *Tambourissa amplifolia* and *T. tau*). Another factor contributing to reproductive isolation between sympatric species is different flowering times, clearly operative in *Monimia* species in Réunion (see section on Habitat and Ecology), and also for Mauritian *Tambourissa* species with common pollinators (e.g., *T. ficus* flowers from September to December; *T. peltata* flowers from March to June). Reproductive isolation appears to be effective, as hybridization is extremely rare in the wild in Mauritius, although artificial crosses resulted in fruit set in three different interspecific combinations (Table 13).

Prolonged flowering periods and high floral output may compensate for low pollinator efficiency. Finally, dioecism and self-sterility in monoecious species can be viewed as representing mechanisms to enforce outcrossing (e.g., Bawa, 1974; Bawa & Opler, 1975). Self-compatibility in *Tambourissa sieberi* most likely offsets low population densities and low efficiency of its small pollinators.

Systematic Treatment

MONIMIACEAE Jussieu, Ann. Mus. Natl. Hist. Nat. 14: 133. 1809 (sub Monimiées).

Evergreen trees or shrubs, rarely lianas, usually aromatic, frequently dioecious or monoecious, sometimes hermaphroditic. Leaves simple, usually opposite and decussate, rarely ternate, alternate or anisophyllous, exstipulate, with laminar oil glands, the trichomes simple, fasciculate and/or stellate, the venation festooned brochidodromous, rarely craspedodromous, the margin entire or serrate to dentate with glandular teeth. Inflorescence cymose or thyrsic, or the flowers fasciculate or solitary, either terminal, axillary, ramiflorous or cauliflorous, the bracteoles small and caducous; flowers small to large, actinomorphic, rarely oblique, bisexual, polygamous or unisexual, the receptacle ± well developed, globose, ovoid to obovoid, urceolate, napiform, campanulate or discoid, the tepals subequal, spiral, whorled or decussate, large and petaloid to small or ± lacking; androecious flowers with few to numerous stamens in 1–many series or irregularly disposed, the filaments usually short and flattened, occasionally with a pair of basal appendages, the anthers erect, (2–)4-sporangiate, the loculi separate or confluent apically or rarely basally, lateral or ± unifacial, valvate or longitudinally dehiscent; gynoecious flowers with or without staminodes, the carpels several to numerous, rarely solitary, unilocular, shortly stalked or sessile, free or enclosed or immersed in the receptacle wall, the style short or elongated, the stigma terminal, dry or secreting mucilage, the ovule solitary, erect, horizontal or pendulous. Fruiting carpels exposed, or enclosed or immersed in the accrescent receptacle wall, indehiscent, often drupaceous with a membranous or fleshy mesocarp and/or aril-like appendage, or plumose (Atherospermoideae); endocarp membranous to bony, the seed erect to pendulous, the testa membranous, the endosperm abundant, oily and fleshy, the embryo straight, the cotyledons erect or divaricate.

The Monimiaceae sensu lato include the subfamilies Atherospermoideae, Hortonioideae, Siparunoideae, Monimioideae, and Mollinedioideae, and comprise some 30 genera and nearly 350 species in the tropics and subtropics, with the greatest diversity occurring in the southern hemisphere.

Key to Genera of Monimiaceae in the Malagasy Region

1a. Trichomes of leaf and stem in part or all stellate with 4–16 horizontal rays, the others simple or in fascicles of 2–4; abaxial laminar surface obscured by a dense, whitish indu-

ment of trichomes; stamens bearing a pair of appendages on filament (Monimioideae) ..... 1. *Monimia*

1b. Trichomes of leaf and stem either simple or rarely in fascicles of 2–4, never stellate; abaxial laminar surface visible, not obscured by trichomes; stamens lacking appendages on filament (Mollinedioideae).

2a. Gynoecious receptacle flat and discoid to ± concave, the carpels superior, subsessile to sessile, free on the disc, clavate to columnar; fruiting receptacle ± discoid, concave to convex, bearing the exposed, ± free drupes, not splitting at maturity.

3a. Buds and flowers with 7–15 large, thick obtuse tepals imbricate in 1–2 radial series; male floral receptacle unfolding gradually at anthesis, not splitting ..... 2. *Decarydendron*

3b. Buds and flowers with 4–8(–16) small to minute decussate tepals; male floral receptacle splitting into 4 valvate segments at anthesis ..... 3. *Ephippiandra*

2b. Gynoecious receptacle ± urceolate, cupuliform to napiform, ellipsoid or cylindric (discoid in *T. peltata*), the carpels inferior, syncarpous, immersed in the receptacle wall; fruiting receptacle ± closed, the drupes immersed in the wall, splitting open irregularly at maturity ..... 4. *Tambourissa*

Monimia Thouars, Hist. Vég. Iles France 35, tab. 9. 1804; Thouars, Hist. Vég. Iles Austral. Afriq. ed. 1: 35, tab. 9. 1805; Willd., Sp. Pl. 4(2): 647. 1805; Juss., Ann. Mus. Natl. Hist. Nat. 14: 116. 1809; Poir., Encycl. Suppl. 3: 726. 1813; Spreng., Syst. 3: 906. 1826; Boj., Hortus Maurit. 289. 1837; Tul., Monogr. Monim. 307. 1855; A.DC., Prodr. 16(2): 661. 1868; Baill., Adansonia, Ser. 1, 9: 133. 1868–1870; Baill., Hist. Pl. ed. 2, 1: 299. 1871; Benth. & Hook., Gen. Pl. 3: 139. 1883; Baker, Fl. Mauritius 289. 1877; Hobein, Bot. Jahrb. Syst. 10: 56. 1889; Pax, Pflanzenfam. 3(2): 101. 1891; Cordem., Fl. Réunion 299. 1895; Perk. & Gilg, Pflanzenr. 4, 101: 65. 1901; Perk, Pflanzenr. 4, 101 (Nachtr.): 39. 1911; Vaughan, Mauritius Inst. Bull. 1: 76. 1937; Hutch., Gen. Fl. Pl. 1: 118. 1964. LECTOTYPE: *M. rotundifolia* Thouars, cf. Bullock, Kew Bull. 14: 44. 1960.

Dioecious pubescent aromatic evergreen trees, rarely shrubby; bud scales present. Leaves opposite, decussate, entire, strongly discolorous, the abaxial surface obscured by a dense indument of simple, fasciculate and/or stellate-peltate trichomes, the venation festooned brochidodromous. Inflorescence pubescent, a thyrse or cyme, rarely leafy, either ramiflorous, axillary or subfoliar on leafless nodes, rarely terminal, the bracts and bracteoles caducous, the flowers borne in umbelloid units of 2–7. Male receptacle pedicellate, obovoid or globose in bud, the apex with several pairs of minute, decussate tepals, splitting at anthesis into 4–6 ± regular valvate segments, tomentose within, the short stamens numerous, multiseriate, the filament thin, subtended by a pair of basal appendages, the connective and filament reddish brown, full of oil cells, blunt or slightly prolonged and rounded, the anther ovoid, bilocular, the loculi separate, parallel, longitudinally dehiscent, introrse; pollen inaperturate, spheroid, spinose. Female receptacle pedicellate, globose-urceolate to ovoid-urceolate, the apex with several pairs of minute decussate tepals, the carpels 4–14 per flower, unilocular, subsessile, free, enclosed within the receptacle which is lined with dense, simple hairs, the styles simple, ± papillose, exserted through the narrow, 3–5-lobed orifice at anthesis, the ovule solitary, pendulous, anatropous. Ripe fruiting receptacle splitting into 3–5 irregular valvate lobes, pinkish red and partly velutinous within, exposing 4–12 ovoid-compressed fruiting carpels (drupes) surrounded by a fleshy orange mesocarp, the apical half covered by a fleshy orange stylar aril, the endocarp whitish, thick, bony, mucronate, and longitudinally crested, the surface foveate, foveate-reticulate to foveate-sulcate.

Distribution. *Monimia* consists of three species endemic to the Mascarene Islands of Mauritius and Réunion. The presence of *Monimia* in Rodrigues is doubtful and based on a single collection of *M. ovalifolia* (*Balfour s.n.*, K). As Balfour failed to mention the genus in his comprehensive work on the botany of Rodrigues (1879), I suspect the specimen is wrongly labelled and may actually have come from Réunion where Balfour also collected. The *Balfour s.n.* collection most closely resembles plants of *M. ovalifolia* from Réunion characterized by orbiculate leaves. Furthermore, Rodrigues does not even attain the minimum altitude at which the species occurs in Mauritius and Réunion.

TAXONOMIC HISTORY OF *MONIMIA*

Monimia was described by A. Du Petit-Thouars in 1804 based on two species, *M. ovalifolia* and *M. rotundifolia,* which he collected in Mauritius and Réunion respectively. Du Petit-Thouars described the genus accurately and not-

ed the close similarity between the androecious flowers of *Monimia* and those of *Tambourissa* (as *Ambora* Juss., and *Mithridatea* Comm. ex Schreb.). As *Monimia* differed from the latter most conspicuously in the structure of its gynoecious flowers, he named it after Monima, wife of Mithridates.

In 1809, Jussieu created a new family (as Monimieae) for *Monimia, Tambourissa* (as *Ambora*), and four other genera of Monimiaceae, which were all previously placed in the Urticaceae by various authors. Willdenow (1805) and Sprengel (1826) placed *Monimia* in subgroups of their "Dioecia," along with other anomalous genera belonging to unrelated families, but followed Du Petit-Thouars in noting its affinities to *Tambourissa.*

In his monograph of the family, Tulasne (1855b) placed *Tambourissa* and *Monimia* in separate tribes. *Monimia* was included in his "Drupaceae" (Monimieae) together with *Siparuna* Aubl. (as *Citrosma* Ruiz & Pav.), *Mollinedia* Ruiz & Pav., *Kibara* Endl., *Hedycarya* Forst., and *Peumus* Mol. (as *Boldea* Juss.) on the basis of their free, drupaceous carpels. Tulasne (1855b) also described an additional species of *Monimia, M. citrina,* which I consider to be synonymous with *M. rotundifolia.* Baillon (1868–1870, 1871) generally followed Tulasne, including *Monimia* under his "*Hortonia* series" (Hortonieae) with many of the same genera as Tulasne, although he included a number of others also having free, drupaceous carpels.

Bentham and Hooker (1883) recognized two large tribes of Monimiaceae on the basis of staminal dehiscence and position of the ovule. They placed *Monimia* with the bulk of genera now included in the Monimiaceae sensu stricto, a treatment largely followed by Hutchinson (1964).

Monimia has been placed in the tribe Monimieae within the subfamily Monimioideae, along with *Tambourissa, Palmeria* F. Muell., and *Hennecartia* Poisson by Pax (1891), Perkins and Gilg (1901), and Perkins (1911). Schodde (1970) created a separate subfamily for *Peumus* based on features of wood, pollen, and chromosome number but ignored *Monimia,* leaving it in the Monimioideae with the bulk of Monimiaceae sensu stricto. More recently, Thorne (1974) joined *Monimia* with *Peumus* as the sole members of the subfamily Monimioideae and created a new subfamily, the Mollinedioideae, to house the remaining genera formerly included in the Monimioideae.

SYSTEMATIC POSITION OF *MONIMIA*

Baillon (1871), Money et al. (1950), and Cavaco (1965) all noted floral morphological similarities between *Monimia* and *Palmeria.* In addition, the wood of *M. ovalifolia* and several species of *Palmeria* shows similar advanced trends (Garratt, 1934; Money et al., 1950). Other shared characters in *Monimia* and *Palmeria* include a dense indument of simple, fasciculate and stellate trichomes, an urceolate gynoecious receptacle enclosing a small number of subsessile or sessile carpels, and a fruiting receptacle which splits open to reveal the ripe carpels set against a pink or red inner surface (Corner, 1976; Endress, 1980b). In spite of superficial similarities in the fruiting receptacles of the two genera, however, which may represent parallel lines of evolution, important differences also exist. The carpels of *Palmeria* are anatomically different from those of *Monimia* and possess a well-developed, hard and shiny black exocarp and thin mesocarp of starch-filled cells absent in the latter (Corner, 1976).

Monimia appears to have closer affinities with *Peumus,* a monotypic genus endemic to Chile. Both genera have horizontal axillary buds, stamens with paired appendages on the filaments, large, spinose pollen grains, the spines and surface composed of cable-like strands (smaller and spinulose in *Palmeria*), receptacles covered by a dense indument of simple, fasciculate and stellate trichomes, carpels with a fleshy mesocarp surrounding the bony white, sculptured endocarp (Fig. 19A, B), and also share the dioecious habit.

In *Peumus,* however, the stamens are tetrasporangiate and dehisce laterally, whereas in *Monimia* they are bisporangiate and dehiscence is nearly introrse along the inner margin (Fig. 13A). In these respects *Monimia* and *Peumus* appear to provide a link between the Atherospermoideae, with their bisporangiate anthers having valvate dehiscence and similar staminal appendages, and the Mollinedioideae, which have tetrasporangiate anthers with lateral dehiscence and lack staminal appendages (Sampson, 1969a, 1969b). As a result, the two genera do not fit satisfactorily into either subfamily.

Specialization in Monimiaceae is generally considered to be expressed in terms of floral simplification and reduction, both in terms of size and number of parts (Money et al., 1950; Endress, 1980b). In these respects, *Monimia* has attained a greater degree of floral morphological

specialization than *Peumus,* in spite of the latter's more specialized wood anatomy (Garratt, 1934; Money et al., 1950; Lemesle & Prichard, 1954). Although also dioecious, *Peumus* has retained a greater constellation of unspecialized floral characters, i.e., an elaborate perianth of whorled petaloid and sepaloid tepals, and a broad, shallow floral receptacle bearing exposed carpels in the manner of the putatively primitive *Hortonia* (Lemesle & Prichard, 1954; Endress, 1980a). Flowers of *Monimia* have reduced, scalelike decussate tepals, are closed in bud, and the female receptacle encloses the carpels—all advanced features.

Similarities which *Monimia* shares with *Peumus,* and to a lesser degree with *Palmeria,* suggest possible origin from a common ancestral stock. A *Monimia* precursor may have originally existed in Africa or Madagascar where it subsequently became extinct, but not before reaching the Mascarene Islands via long distance dispersal. The Mascarenes thus provided a refuge for *Monimia.*

Current work with sieve tube plastid analysis by Behnke (1977, and pers. comm.) has shown that *Palmeria* and *Peumus* possess fundamentally different types of sieve tube plastids (S-type and P-type, respectively). As *Monimia ovalifolia* possesses S-type plastids (Behnke, pers. comm.), this feature at least would seem to deny a close relationship to *Peumus.* Sieve element plastids unquestionably provide an additional taxonomically useful character when used in conjunction with other available data, but do not provide an adequate basis for fragmenting the Monimiaceae into some five families as proposed by Behnke (1981).

In summary, *Monimia* displays a number of advanced features, certain of which (i.e., its stamens) are transitional between the Mollinedioideae and the Atherospermoideae. As *Monimia* shares the greatest constellation of features with *Peumus,* however, the two genera are best placed together as constituting the Monimioideae as proposed by Thorne (1974).

KEY TO THE SPECIES OF *MONIMIA*

1a. Leaves amplexicaul with a deeply cordate base, sessile to subsessile; Réunion ..... 1. *M. amplexicaulis*

1b. Leaves distinctly petiolate, the base neither deeply cordate nor amplexicaul; Réunion and Mauritius.

2a. Stems, petioles and inflorescence hirsute-velutinous; trichomes on adaxial surface of lamina mixed simple, fasciculate and stellate with free, ± ascending arms; Réunion ..... 2. *M. rotundifolia*

2b. Stems, petioles and inflorescence at most scabrous or scurfy, not velutinous; trichomes on adaxial surface of lamina uniformly stellate-peltate with horizontal arms united basally for ⅓–½ their length; Réunion and Mauritius ..... 3. *M. ovalifolia*

1. Monimia amplexicaulis Lorence, Bull. Mus. Hist. Nat. (Paris), Ser. 4, Sect. B, Adansonia 3(3): 294, pl. 1, fig. 1a. 1982. TYPE: Réunion. Hauts du Tévelave: forestry road along the Domanial line, cloud forest transitional to heath formation, ca. 1,700 m, 6 Mar. 1979 (fl, fr), *Lorence 2504* (holotype, MO; isotypes, K, MAU, P, REU, Z).

Shrub or small tree attaining 10 m tall and 30 cm diam., the bark grayish brown, longitudinally fissured, the new growth pale grayish to fulvous, velutinous-tomentose with predominantly short-armed stellate trichomes, mixed with long simple and fasciculate trichomes 0.5–1 mm long, the mature leafy stems 3–5 mm diam., velutinous-tomentose. Leaves opposite, sessile to subsessile; petiole stout, 3–5 mm long by 3–5 mm diam., velutinous-tomentose; lamina subcoriaceous to coriaceous, ovate to broadly ovate, broadly elliptic to suborbiculate, (40–)60–130 mm by (32–)40–110 mm, the apex shortly acute, shortly acuminate, mucronate or rounded, the base deeply cordate, amplexicaul, the secondary veins (4–)5–7 pairs, making a 40–60° angle with the costa, the venation depressed adaxially, visible to 3°, prominent and raised abaxially, visible to 4°, the adaxial laminar surface pubescent with predominantly stellate trichomes with 4–12 short horizontal arms, mixed with varying proportions of long simple and fasciculate trichomes with 2–4 ascendant arms, eventually glabrescent and ± pustular, glandular, the abaxial surface obscured by a dense whitish to pale yellowish indument of the same trichomes, the margin entire, pubescent, plane to slightly revolute. Inflorescence a congested, fulvous velutinous-tomentose thyrse or rarely short cyme of (3–)7–37 flowers (gynoecious inflorescence more congested than the androecious), branching to 2°(–3°), leafy or not, ramiflorous or subfoliar on leafless nodes (the primary axis often continuing to grow as a leafy stem), axillary or rarely terminal, the floral axis (5–)10–60(–75) mm by 2–3 mm, often subtended by 1–several pairs of caducous, brown ciliate-pubescent naviculate bracts to 7 mm by 3 mm,

the peduncle 4–12 mm long, bearing an umbelloid unit of (2–)3(–6) flowers, occasionally subtended by a caducous, velutinous bracteole to 2 mm long or by a small leaf. Androecious flower in bud ellipsoid to obovoid, 2–7 mm long by 3–5.5 mm diam., velutinous-tomentose, the pedicel 3–7 mm by 1–1.5 mm, often subtended by 1–2 minute subulate bracteoles; at anthesis deeply 3–6-fid, 10–13 mm diam., the lobes ultimately reflexing; stamens (40–)60–150, 1.5–2.5 mm long, the anthers ellipsoid, ca. 1 mm wide, occupying ca. ⅓–½ total length of the stamen, the connective slightly prolonged and rounded, the internal receptacle surface tomentose, the simple hairs 0.3–0.8 mm long. Gynoecious flower in bud globose-urceolate to ovoid-urceolate, 4–5 mm long by 3–4 mm diam., at anthesis the orifice 0.8–1.2 mm diam., the styles 5–10, exserted for 1–2 mm, the internal receptacle surface velutinous with simple hairs 0.5–1.5 mm long, the pedicel 1.5–2.5 mm by 1–1.5 mm. Fruiting receptacles in clusters of 1–10 on the leafless branches, ovoid to subglobose, 7–15 mm diam., externally pubescent with stellate, fasciculate and simple trichomes, the carpels 1–10 per receptacle, ovoid to ellipsoid, 5–7 mm long by 3–5 mm thick, mucronate, with a longitudinal crest, the endocarp deeply foveate-reticulate. Figure 21.

Distribution. Endemic to Réunion (Fig. 22).

Habitat. Monimia amplexicaulis is occasional to abundant locally as a component of mid to upper level cloud forest and lower limits of the *Philippia* heath formations from ca. 1,400 to 2,100 m. It is most frequent on the sheltered, leeward escarpments of the "cirques," e.g., at Petit Matarum, Coteau Kerveguen above Cilaos, Hauts du Tévelave, etc.

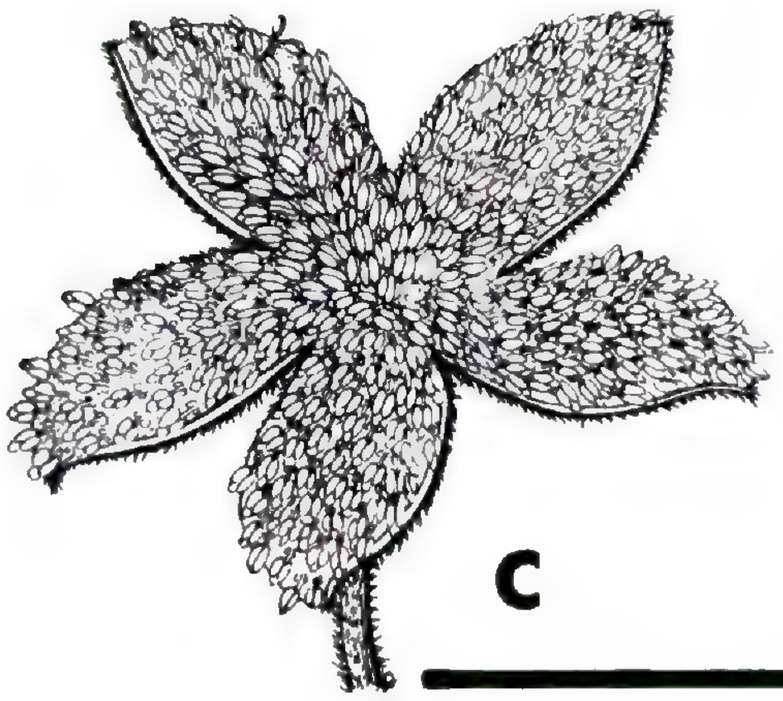
RÉUNION. CIRQUE DE CILAOS: ascent to Col de Taibit, 22 Mar. 1974 (fr), *Bosser 21677* (P); Plaine des Fraises, below Col de Taibit, 1,900 m, 2 Feb. 1967 (fl), *Cadet 663 bis* (REU); Cilaos to Col de Taibit, 1,950 m, 22 Mar. 1974 (fr), *Coode 2558B* (K); Montée Cilaos, Coteau Kerveguen, Feb. 1971 (fl, fr), *Bosser 20752* (P); path to Coteau Kerveguen, 1,500 m, 16 Nov. 1973 (fr), *Cadet 4512* (REU); Coteau Kerveguen, 1,500–1,700 m, 24 Feb. 1979 (fl), *Lorence & Rolland 2443* (MAU, MO); (fl), *Lorence & Rolland 2444* (MAU, MO); forest of Mare à Joseph, 1,400 m, 10 Jan. 1967 (fl), *Cadet 663* (REU); 1,200–2,000 m, Aug. 1943 (fl), *Rivals s.n.* (TL-R); 2,000 m, 11 June 1943 (fr), *Rivals s.n.* (TL-R); wet forest at Petit Matarum, 2,000 m, 22 Feb. 1975 (fl, fr), *Cadet 5049* (REU); (fl), *Cadet 5050* (REU); 4 Feb. 1968 (fl), *Capuron 28210-SF* (P); 6 Mar. 1971 (fl), *Friedmann 1118* (P); (fr), *Friedmann 1119* (P); path to Piton des Neiges, 15 Apr. 1978 (fl, fr), *Bosser 22498* (P); 28 Mar. 1973 (fr), *Lorence sub MAU 15693* (MAU); (fl, fr), *Rivals s.n.* (TL-R). CIRQUE DE MAFATE: Col de Fourche, 1,800 m, 29 May 1976 (fr), *Cadet 5435* (REU); valley of Bras Bémale, 1,500 m, 13 May 1976 (st), *Cadet 5404* (REU); above Belier, on Sentier des Scouts to Aurère, 1,500 m, 14 May 1976 (st), *Richardson 4132* (K). PLAINE DES CAFRES: base of Piton Bleu, 1,500 m, 11 July 1943 (fl), *Rivals s.n.* (TL-R); (fr), *Rivals s.n.* (TL-R); 24 Feb. 1945 (fr), *Rivals s.n.* (TL-R); path to Coteau Maigre, 2,100 m, Feb. 1971 (fl), *Bosser 20475* (P). PLAINE DES CHICOTS: 1,900 m, 19 Feb. 1945 (fr), *Rivals s.n.* (TL-R). PLAINE DES MERLES: Cirque de Salazie near La Nouvelle (sic), 1,300 m, 17 Feb. 1944 (fl), *Rivals s.n.* (TL-R). PLAINE DES SALAZES: Sources Bras Cabot, 17 Aug. 1944 (st), *Rivals s.n.* (TL-R). PLAINE DES TAMARINS: 20 Aug. 1944 (st), *Rivals s.n.* (TL-R). HAUTS DU TÉVELAVE: 1,700 m, 21 Sept. 1974 (fr), *Cadet 4797* (REU); (fl), *Cadet 4797 bis* (REU); along the Domanial line, 1,700 m, 6 Mar. 1979 (st), *Lorence 2501* (MO); (fl), *Lorence 2502* (MAU, MO); (fl, fr), *Lorence 2503* (MAU, MO).

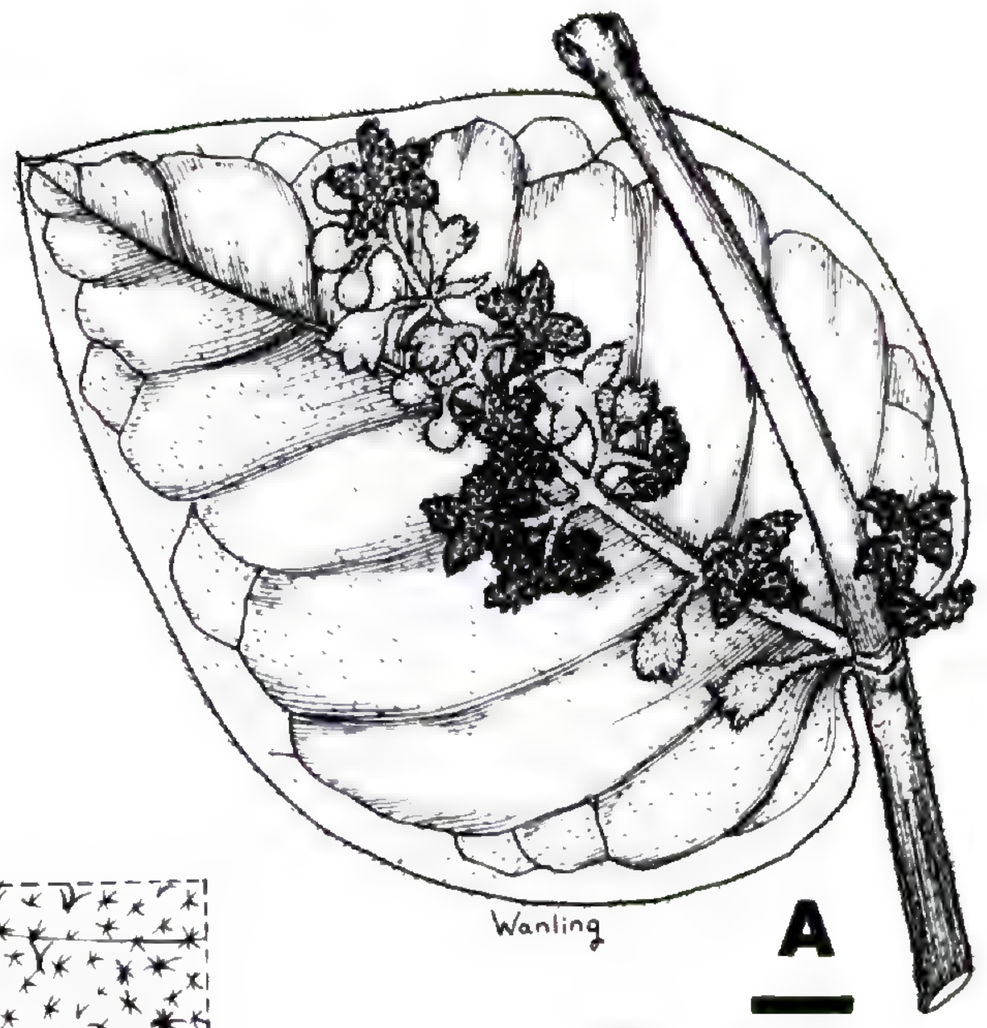
Monimia amplexicaulis shares morphological features with *M. rotundifolia,* including the presence of three types of foliar trichomes (stellate, fasciculate, and simple; Fig. 9A). In *M. amplexicaulis,* the trichomes are predominantly stellate with short arms and not predominantly long, fasciculate and simple as in *M. rotundifolia. Monimia amplexicaulis* further differs from the latter by its sessile, deeply cordate, and amplexicaul leaves with 5–7 secondary veins and generally occurs at somewhat higher elevations in more sheltered habitats than *M. rotundifolia,* often at the cloud forest/heath formation interface.

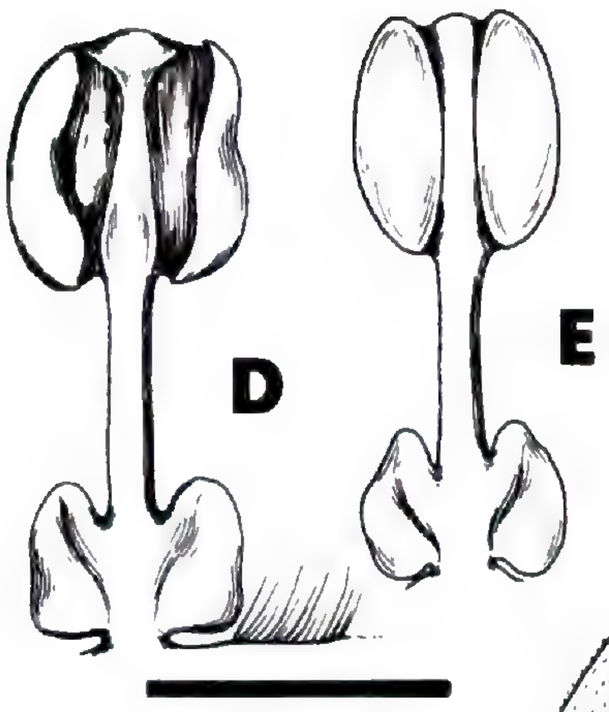
Vernacular names. Mapou, Mapou des hauts (Réunion).

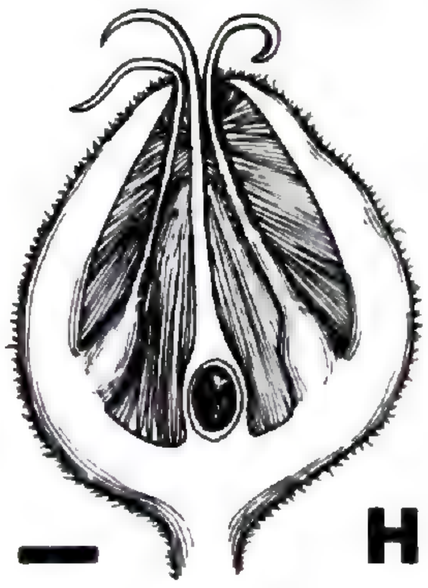
2. **Monimia rotundifolia** Thouars, Hist. Vég. Iles France 35, tab. 9, fig. 2. 1804; Thouars, Hist. Vég. Iles Austral. Afriq. 21, 34, tab. 7, fig. 2. 1805; Willd., Sp. Pl. 4(2): 647. 1805; Spreng., Syst. 3: 906. 1826; Poir., Encycl., Suppl. 3: 727. 1843; Tul., Ann. Sci. Nat. (Paris) 4(3): 32. 1855; Tul., Monogr. Monim. 310, tab. 29a–j. 1855; A.DC., Prodr. 16(2): 661. 1868; Cordem., Fl. Réunion 299. 1895; Perk. & Gilg, Pflanzenr. 4, 101: 66, fig. 18A–D. 1901; Perk., Pflanzenr. 4, 101 (Nachtr.): 39. 1911 (excluding *Balfour s.n.* collection from Rodrigues); Perk., Gatt. Monim. fig. 34A–D. 1925. TYPE: Ile Bourbon (Réunion). Without precise locality (ca. 1800–1801), *Petit-Thouars s.n.* (holotype, P).

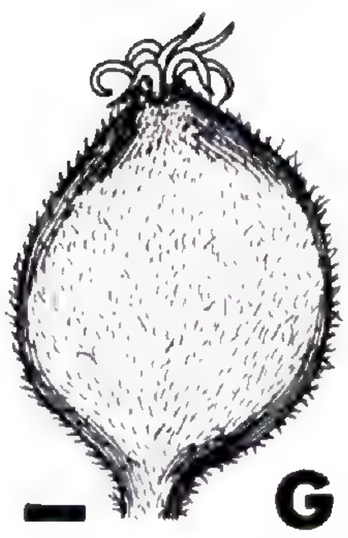
Ambora tomentosa Bory, Voy. Iles Afrique 1: 317, tab. 13. 1804. *Myrtus villosa* Spreng., Syst. 2: 487.

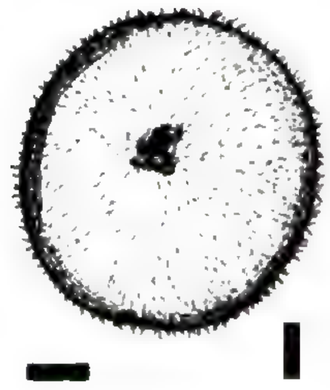












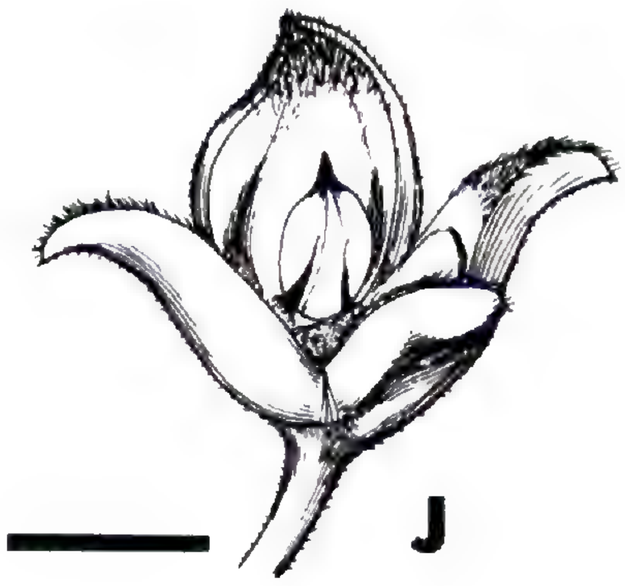


FIGURE 21. *Monimia amplexicaulis* Lorence.—A. Habit, male, one leaf removed.—B. Detail of adaxial leaf surface.—C. Androecious flower at anthesis.—D. Stamen, adaxial view.—E. Stamen, abaxial view.—F. Habit, female.—G. Gynoecious flower at anthesis, lateral view.—H. Gynoecious flower at anthesis, longitudinal section.—I. Gynoecious flower, apical view to show pore (styles removed).—J. Ripe fruiting receptacle, dehisced.—K. Fruiting carpel, lateral view. A–E. *Lorence 2444* (MO). F, J, K, *Lorence 2404* (MO). G–I. *Lorence 2503* (MO). Bars equal 10 mm in A–C, F, J, and 1 mm in D, E, G–I, K.

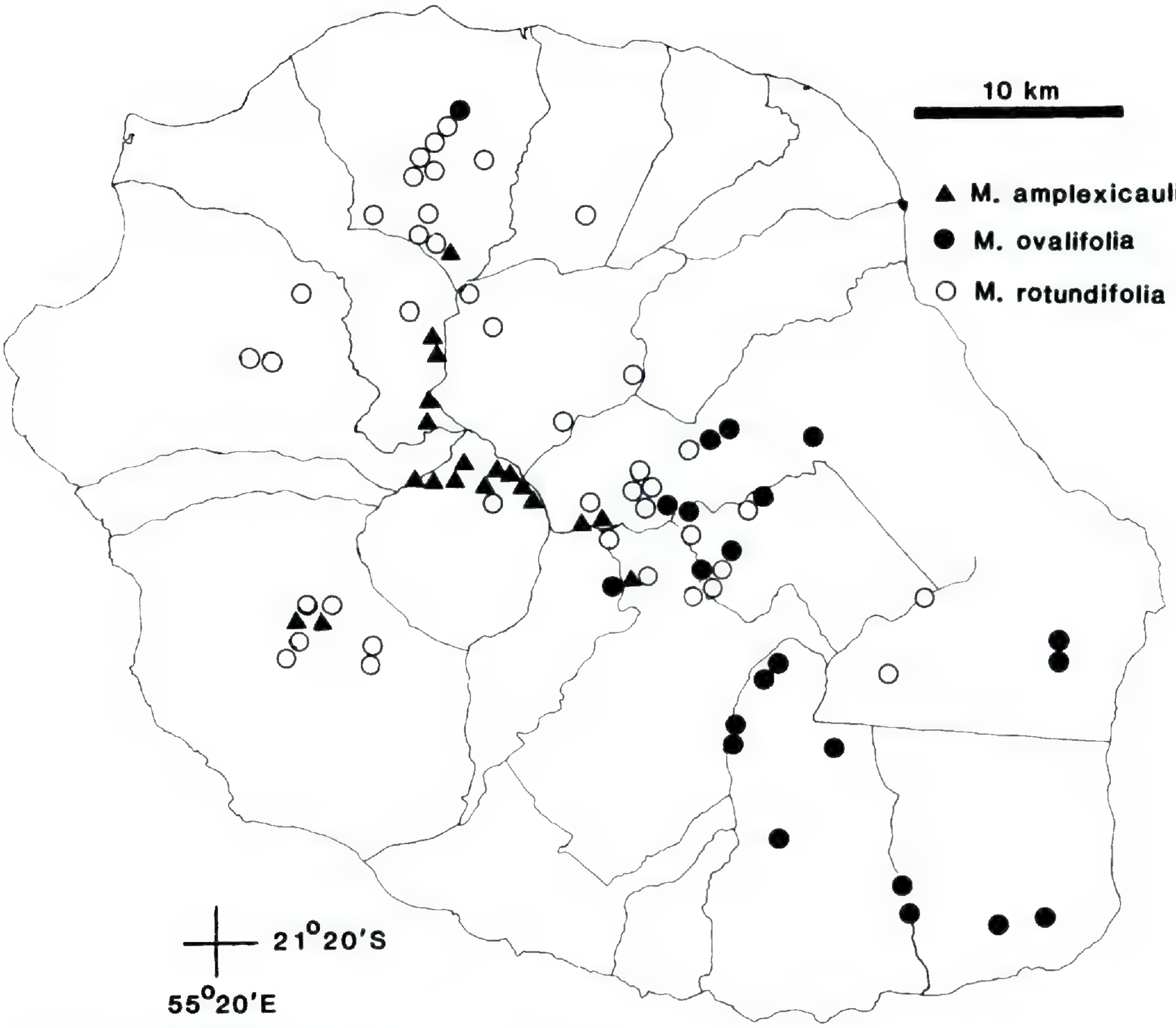


FIGURE 22. Distribution map of *Monimia* in Réunion.

1825, nom. superfl., based on type of *Ambora tomentosa* Bory. *Eugenia villosa* (Spreng.) Poir., Encycl., Suppl. 3: 124. 1843, nom. superfl. TYPE: without precise locality (probably Réunion), *Bory de St. Vincent s.n. in 1821* (holotype, G-DC, n.v.; microfiche, MO).

Monimia citrina Tul., Ann. Sci. Nat. (Paris) 4(3): 32. 1855; Tul., Monogr. Monim. 311. 1855; A.DC., Prodr. 16(2): 661. 1868; Perk. & Gilg, Pflanzenr. 4, 101: 65. 1901. TYPE: Ile de Bourbon (Réunion): without precise locality, *Gaudichaud s.n. in 1836–1837* (lectotype, P, here designated; isolectotype, P).

M. ovalifolia sensu Cordem., Fl. Réunion 300. 1895 non Thouars.

Shrub or low tree attaining 10 m tall and 60 cm diam., the new growth velutinous-tomentose, pale gray to fulvous, the simple and fasciculate trichomes 0.5–1 mm long, mixed with short stellate trichomes, the mature leafy stems 3–6 mm diam., velutinous-tomentose. Leaves petiolate; petioles 5–20 mm by 2–4 mm, velutinous-tomentose; lamina coriaceous, ovate to broadly ovate, elliptic to broadly elliptic or orbiculate, (35–)45–150 mm by (23–)35–160 mm (attaining 320 mm by 300 mm on vigorous sucker shoots), the apex shortly acuminate, acute, mucronate, obtuse, rounded or rarely retuse, the base acutely decurrent, acutely cuneate, obtuse, rounded or shallowly cordate, the secondary veins 3–7 pairs, making a 45–60° angle with the costa, the venation depressed adaxially, visible to 3°, abaxially raised and visible to 4°, the adaxial laminar surface strigose-hirsute, generally with predominantly long, simple hairs and fasciculate trichomes with 2–4 long, ascendant arms, mixed with varying proportions of stellate trichomes with 4–12 shorter horizontal arms, the surface glandular, eventually ± pustular, the abaxial laminar surface obscured by a dense, whitish to pale yellowish indument of the same trichomes, the margin entire, pubescent, plane to slightly

revolute. Inflorescence a congested to lax thyrse (rarely a short cyme) of (3–)6–76 flowers (the gynoecious inflorescence more congested than the androecious), branching to 2–3°, leafy or not, velutinous-tomentose, either ramiflorous, subfoliar on leafless nodes (the primary axis sometimes continuing to grow as a leafy shoot), or axillary, the floral axis (7–)15–90(–130) mm by 1.5–2.5 mm, often subtended by 1–4 pairs of brown, scale-like, pubescent or ciliate bracts to 10 mm by 4 mm, the secondary axes 2–25(–50) mm long, occasionally subtended by a single caducous brown bracteole 2–3 mm long, the peduncle 2–12 mm long, bearing an umbelloid unit of 2–6 flowers. Androecious flower in bud ellipsoid, obovoid or subglobose, 4.5–8 mm by 3–5 mm, velutinous-tomentose, the pedicel 3–13 mm by 0.5–1 mm, often subtended by 1–2 minute bracteoles; at anthesis deeply 3–5-fid, 4–14 mm diam., the lobes ultimately reflexing; stamens (25–)50–105, 2–3.5 mm long, the anther 1–1.4 mm wide, ellipsoid, occupying ¼–½ total length of the stamen, the connective ± thickened, blunt or slightly apiculate, the internal receptacle surface tomentose, the hairs simple. Gynoecious flower in bud ovoid-urceolate to globose-urceolate, 3.5–5 mm by 2.5–4 mm; at anthesis the orifice 1–1.2 mm diam., the styles 5–10, exserted for 1–2 mm, the internal receptacle surface velutinous, the short hairs simple, the pedicel 1.5–5 mm by 1–1.5 mm. Fruiting receptacles borne in clusters of 1–20 on leafy or leafless branches, ovoid to subglobose, 6–14 mm diam., externally pubescent with simple, stellate and fasciculate trichomes, the carpels 1–8 per receptacle, ovoid, 6–8 mm long, 4–6 mm wide, 4–5 mm thick, mucronate with a longitudinal crest, the endocarp thick, the surface deeply foveate, foveate-reticulate or foveate-sulcate.

Distribution. Endemic to Réunion (Fig. 22).

Habitat. *Monimia rotundifolia* is an occasional to locally abundant component of the cloud forest zone, rarely ranging into the *Philippia* heath zone, from ca. 1,000 to 2,000 m.

RÉUNION. BELOUVE: Apr. 1956 (fr), *Bosser 7586* (P); 1,500 m, Apr. 1956 (fr), *Bosser 9354* (P). BOIS DE NÈFLES: 1,500 m, 17 Sept. 1974 (fl), *Cadet 4787* (REU); (fl), *Cadet 4788* (REU); (fl), *Cadet 4789* (REU). BOUCAN-LAUNAY: woods above Boucan-Launay (fr), *Boivin 1120* (P). BRETAGNE: above Bretagne, 1,000 m, July 1945 (fr), *Rivals s.n.* (TL-R). BRÛLÉ DE ST. DENIS: 1,300 m, May 1957 (fl), *Bosser 11577* (P); 1,000 m, 22 Oct. 1973 (fr), *Bosser 21332* (P, 2 sheets); near Mamode Camp, 1,200 m, 13 Apr. 1968 (fr), *Cadet 1333* (REU); vicinity of Mamode Camp, at Plaine des Chicots, 31 Jan. 1968 (fr), *Capuron 28161-SF* (P, 2 sheets); St. Francois, St. Denis (fr), *Cordemoy s.n.* (TL-R); 1,000–1,200 m, Oct. 1956 (st), *Rivière s.n.* (P). BÉBOUR: Bébour Forest, 4,500 ft. (ca. 1,350 m), 17 Nov. 1967 (fl), *Barclay 554* (K, MAU); Bébour Pass and Rivière des Marsouins, 1,350 m, 21 Oct. 1973 (fl), *Bernardi 14530* (BM, G, P); Bébour Plateau, 1,200–1,300 m, June 1957 (fl), *Bosser 11488* (P, 2 sheets); 1,300 m, 27 Nov. 1973 (fl), *Cadet 4531* (REU); 26 Oct. 1974 (fl, fr), *Cadet 5197A* (REU); 29 May 1975 (fl), *Cadet 5197B* (REU); Bébour Peak, 1,700 m, 27 Nov. 1973 (fl), *Coode et al. 4231* (K, 2 sheets; REU); (fl), *Coode et al. 4235* (K); (fr), *Coode et al. 4237* (K, REU); (fl), *Coode et al. 4238* (K, 2 sheets; REU); 16 Dec. 1970 (fl, fr), *Friedmann 875* (P); 1,400 m, Nov. 1972 (fl, fr), *Friedmann 1982* (P); 1,300–1,600 m, 23 Feb. 1979 (fl), *Lorence 2429* (MO); 1,300 m, 6 May 1976 (fl), *Richardson et al. 4086* (K, MO); (fl), *Richardson et al. 4087* (K, MO); (fl), *Richardson et al. 4088* (K, 2 sheets; MO). CIRQUE DE CILAOS: Petit Matarum, 6 Mar. 1971 (fr), *Friedmann 1119* (P); Cilaos at Matarum, 1,300 m, June 1943 (fl), *Rivals s.n.* (TL-R). CIRQUE DE MAFATE: Sentier des Scouts, crest above Ilet à Malheur, 1,200 m, May 1976 (fr), *Richardson et al. 4138* (K, 2 sheets). CIRQUE DE SALAZIE: path from Grand Ilet to Roche Ecrite, 1,900 m, 15 Oct. 1974 (fl, fr), *Cadet 4836* (REU); below Grand Ilet at Salazie, 1,600 m, 26 Sept. 1977 (fl), *Cadet 5254* (REU); (fl), *Cadet 5255* (REU); Terre Plate, 1,600 m, 7 Apr. 1976 (st), *Cadet 5334* (REU). MAÏDO: road to Maïdo above Petit France, 1,200 m, 22 Feb. 1979 (fr), *Lorence & Cadet 2413* (MAU, MO); Maïdo to Le Guillaum road, 1,550 m, 12 May 1976 (fr), *Richardson et al. 4121* (K, MO); (fl), *Richardson et al. 4122* (K). MASSIF DE LA FOURNAISE: below the shelter at Pas de Bellecombe, 2,000 m, 25 July 1962 (fl), *Cadet 202* (REU). MORNE DE PATATES À DURAND: 1,200 m, Hauts du Bois de Nèfles à St. Denis, 11 Sept. 1976 (fl), *Cadet 5242* (REU); (fl), *Cadet 5243* (REU). PLAINE D'AFFOUCHES: June 1945 (fl), *Rivals s.n.* (TL-R). PLAINE DES CAFRES: open heathland, 5,200 ft. (ca. 1,700 m), 2 Aug. 1968 (fl), *Barclay 471* (K, MAU); Sentier Coteau Maigre, Feb. 1971 (fl, fr), *Bosser 20476* (P); Piton Mare a Bouc, 1,600 m, 7 Nov. 1966 (fl), *Cadet 503* (P, REU); foot of Piton Lepervanche, 1,700 m, 26 Oct. 1974 (fl), *Cadet 4859* (REU); Col de Bellevue, 30 Nov. 1974 (fl), *Friedmann 781* (P); (fl), *Friedmann 782* (P); Col de Bellevue, 1,600 m, 27 Feb. 1979 (fl, fr), *Lorence 2471* (MAU, MO); (fl), *Lorence 2472* (MAU, MO); (fl), *Lorence 2473* (MAU, MO); (st), *Lorence 2474* (MO); 17 July 1979 (fl, fr), *Lorence 2773* (MO, Z); (fl), *Lorence 2774* (K, MO, Z); (fl), *Lorence 2775* (K, MAU, MO, Z); base of Piton Bleu, 11 June 1943 (st), *Rivals s.n.* (TL-R); Grande Montée, mid and upper parts, 12 June 1943 (fl), *Rivals s.n.* (TL-R); lower part of forest at La Grand Montée, 1,200 m (st), *Rivals s.n.* (TL-R); scrub and cloud forest, 1,700 m, 5 Nov. 1966 (fl), *Schlieben 10859* (B, MAU); Grand Montée, 1,600 m, 28 May 1964 (fl), *Staub sub MAU 11105* (MAU); Grand Montée, 4,500 ft. (ca. 1,500 m), 10 Oct. 1960 (fl), *Wiehe sub MAU 1534* (MAU); 1,600 m, 27 Nov. 1964 (fl), *Wiehe sub MAU 11479* (MAU, 2 sheets). PLAINE DES CHICOTS: Roche Ecrite, 1,700–2,277 m, 8 Jan. 1975 (fl), *Bernardi 14936* (P); (fl), *Bernardi 14943* (P); Roche Ecrite, moist forest, 1,300 m, 23 July 1961 (st), *St. John 26527* (G, 2 sheets; K).

PLAINE DES MAKES: 1,100 m, June 1957 (fl), *Bosser 12216* (P); 1,400 m, 6 Apr. 1975 (st), *Cadet 5154* (REU). PLAINE DES PALMISTES: mountainous regions (fl), *Cordemoy s.n.* (TL-R); Petite Plaine above Plaine des Palmistes, 1,200 m, 25 Feb. 1979 (fr), *Lorence & Rolland 2453* (MO). PLAINE DES SALAZES: high altitude ericoid vegetation, Apr. 1957 (fr), *Alphonsine s.n.* (P). RIVIÈRE DE L'EST: far up the Rivière de l'Est, 1,750 m, Nov. 1976 (fl), *Cadet 5710* (REU); (fl), *Cadet 5711* (REU). RIVIÈRE DES REMPARTS: Roche Plate path, 6,500–6,700 ft. (ca. 2,100 m), 16 Nov. 1967 (fl), *Barclay 498* (K, MAU); ca. 5,400 ft. (ca. 1,700 m), 20 Nov. 1968 (fl, fr), *Barclay 1272* (K, MAU); Vallée de la Rivière des Remparts, 1,700 m, 20 Nov. 1968 (fl, fr), *Cadet 1727* (REU); 7 Mar. 1975 (fl), *Cadet 5103* (REU); (fr), *Cadet 5104* (REU); (fr), *Cadet 5105* (REU). SAINTE AGATHE: 19 July 1875 (fl), *De L'Isle 383* (K; P, 2 sheets). SAINTE MARIE: Hauts de Sainte Marie, 1,200 m, 18 Apr. 1976 (fl), *Cadet 5511* (REU). TAKAMAKA: 900 m, 10 Mar. 1979 (st), *Lorence & Rolland 2532* (MAU, MO). TÉVELAVE: Hauts du Tévelave, 1,500 m, 21 May 1975 (fr), *Bosser 22189* (P, 2 sheets); 1,300 m, 5 Sept. 1975 (fl), *Cadet 5255* (REU); ca. 1,500 m, 25 Nov. 1968 (fl), *Edgerley E4 sub MAU 13372* (MAU); May 1976 (fl), *Friedmann 2817* (P); forestry road above Tévelave, 1,300–1,400 m, 28 Feb. 1979 (fr), *Lorence 2477* (MAU, MO); 1,700 m, 6 Mar. 1979 (fl), *Lorence 2505* (MAU, MO); (fr), *Lorence 2506* (MAU, MO). WITHOUT PRECISE LOCALITY: (fl), *Anon. ex Herb. Kopp s.n.* (P, 3 sheets); (fl), *Anon. ex Herb. Station Agronom. Réunion s.n.* (P, 2 sheets); (fl), *Armange 20* (P); (fr), *Balfour s.n.* (K); (fl), *Barthe s.n.* (P); (fr), *Boivin 1120* (G, 2 sheets; P, 2 sheets); (fl, fr), *Boivin s.n.* (G; P, 3 sheets); (fl), *Bory de St. Vincent s.n.* (G-DC, microfiche); (fl), *Commerson s.n.* (BM, G, P; syntypes of *M. citrina*); (fl), *Commerson s.n.* (P); (fl), *De L'Isle s.n.* (P); (fl), *Gaudichaud s.n.* (G, P; syntypes of *M. rotundifolia*); (fl, fr), *Gaudichaud s.n.* (K, P); (fl), *Gaudichaud s.n. in 1837* (G); (st), *Giraudy s.n. in 1847* (P); (fl), *Monssi (?) s.n. in 1833* (P); (fl, fr), *Potier s.n.* (P, 3 sheets); (fl), *Richard 2* (K); (fl, fr), *Richard s.n.* (P, 3 sheets); (fl, fr), *Richard 27* (P, 2 sheets). LOCALITY (ISLAND) UNKNOWN: (fl), *Anon. sub Herb. ORSTOM 4999* (MAD); (fl), *Anon. sub MAU 2993* (MAU).

Monimia rotundifolia is an extremely variable species as to size and shape of the lamina, although its leaves are never sessile to subsessile and deeply cordate-amplexicaul as in *M. amplexicaulis*. Composition of laminar trichomes is also a variable feature. Long simple hairs predominate on the adaxial leaf surface of many individuals (e.g., Fig. 9C), but in others large numbers of long fasciculate and shorter stellate trichomes are present (e.g., Fig. 9B), approaching the condition found in *M. amplexicaulis*. Bojer (1837), followed by Baker (1877), erroneously stated that *M. rotundifolia* occurred in Mauritius, but cited no collections, and no authentic specimens are known from Mauritius. Its wood is occasionally used for construction in Réunion and is said to be virtually incombustible.

Vernacular names. Mapou, Mapou à grandes feuilles, Mapou blanc, Mapou des hauts (Réunion).

3. Monimia ovalifolia Thouars, Hist. Vég. Iles France 35, tab. 9, fig. 1. 1804; Thouars, Hist. Vég. Iles Austral. Afriq. 21, 34, tab. 7, fig. 1. 1805; Willd., Sp. Pl. 648. 1805; Spreng., Syst. 3: 906. 1825; Bojer, Hortus Maurit. 289. 1837; Poir., Encycl., Suppl. 3: 727. 1843; Tul., Monogr. Monim. 309. 1855; A.DC., Prodr. 16(2): 661. 1868; Baker, Fl. Mauritius 289. 1877; Cordem., Fl. Réunion 300. 1895; Perk. & Gilg, Pflanzenr. 4, 101: 65, fig. 18E–F. 1901; Perk., Gatt. Monim. fig. 34E–F. 1925; Vaughan, Mauritius Inst. Bull. 1: 76. 1937. TYPE: Ile de France (Mauritius). Without precise locality (ca. 1800–1801), *Petit-Thouars s.n.* (lectotype, P, here designated; isolectotypes, P, 2 sheets).

M. ovalifolia var. *boryana* A.DC., Prodr. 16(2): 661. 1868. TYPE: without precise locality (probably Mauritius or Réunion) (ca. 1821), *Bory de St. Vincent s.n.* (holotype, G-DC, n.v.; microfiche, MO).

M. citrina sensu Cordem., Fl. Réunion 300. 1895 non Tul.

M. rotundifolia sensu Perk., Pflanzenr. 4, 101 (Nachtr.): 39. 1911 non Thouars, as to *Balfour s.n.* collection from Rodrigues (K).

Shrub or small tree 7–15 m tall and 40 cm diam., the bark pale brown, smooth, flaking, the new growth scurfy-pubescent, the mature leafy stems scurfy to scabrous, glabrescent, 2.5–5 mm diam., the stems, petioles, costa, and inflorescence axes scabrous to scurfy with mostly small, appressed stellate-peltate trichomes with 8–16 short, horizontal arms, mixed with fewer simple hairs and fasciculate trichomes with 2–8 long, ascendant arms. Leaves opposite, petiolate; petioles (3–)5–25 mm by 2–4 mm; lamina subcoriaceous to coriaceous, ovate-elliptic, elliptic, broadly elliptic, suborbiculate or orbiculate, occasionally obovate, (30–)50–130(–170) mm by (20–)30–110(–153) mm (attaining 200 mm by 200 mm with petioles 35 mm long on vigorous sucker shoots), the apex shortly acuminate, shortly acute, obtuse, rounded or retuse, the base acutely decurrent, acute, obtuse, rounded or shallowly cordate, the secondary veins 4–7 pairs, making a 50–65° angle with the costa, the venation depressed adaxially and visible to 2(–3°), raised abaxially and visible to 3(–4°), the adaxial laminar surface scabrous with scattered, ± ap-

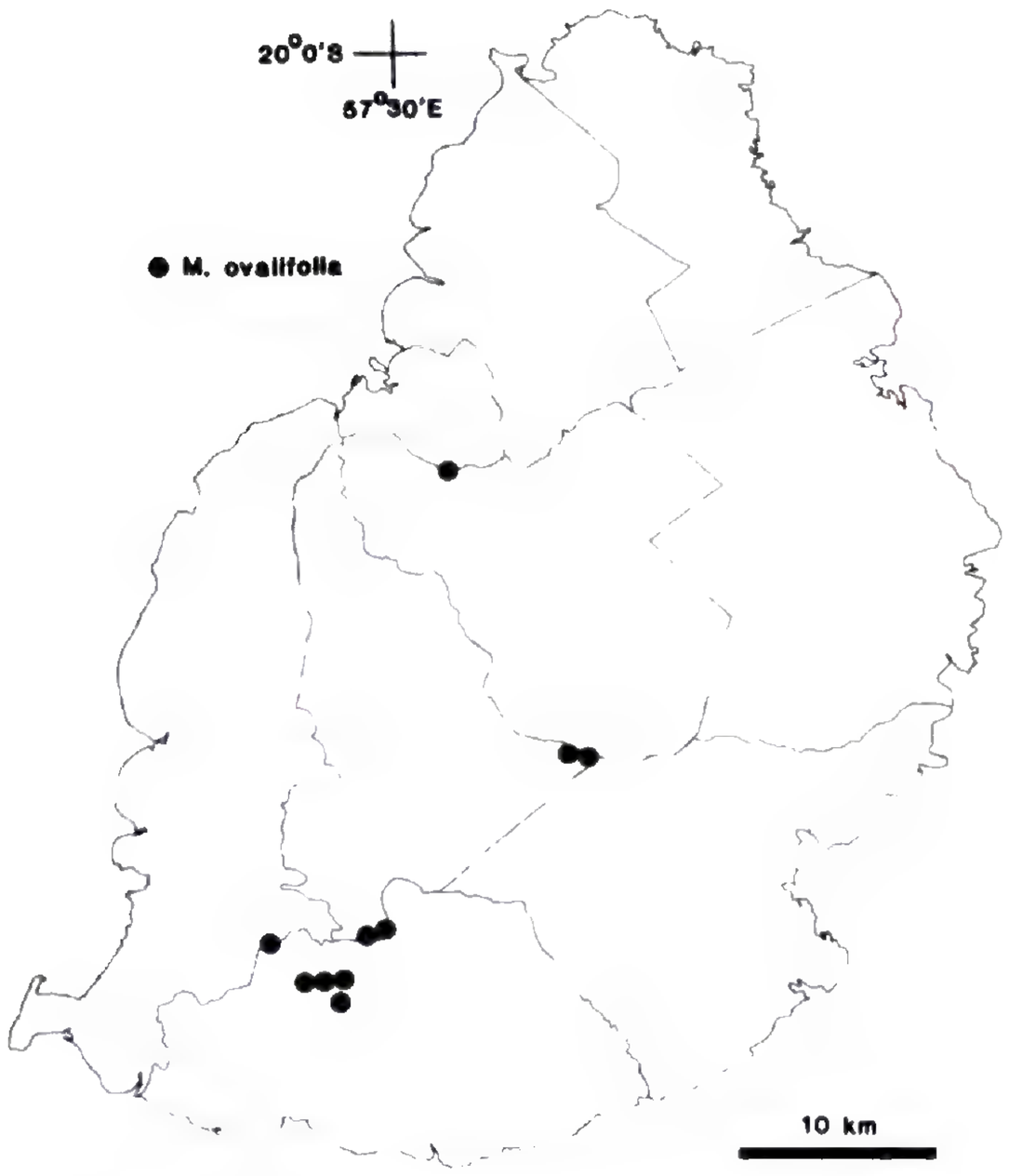


FIGURE 23. Distribution map of *Monimia* in Mauritius.

pressed stellate-peltate trichomes with 6–16 short, horizontal arms, the costa and secondary veins with scattered simple and fasciculate trichomes, eventually glabrescent and ± pustular, glandular, the abaxial laminar surface obscured by a dense whitish indument of the same trichomes, the margin entire, plane to slightly revolute. Inflorescence a scurfy to scabrous thyrse (rarely a short cyme or pleiochasium) of (3–)8–87 flowers, branching to 2(–3°), leafy or not, ramiflorous, either subfoliar on leafless nodes (the primary axis sometimes continuing to grow as a leafy stem), axillary, or rarely terminal, the floral axis (5–)10–120(–165) mm by 1.5–3 mm, often subtended by 1–several pairs of caducous brown, ciliate to pubescent naviculate bracts to 7 mm by 3 mm, the peduncle 3–20 mm by 0.5–1 mm, often subtended by a single caducous brown bracteole 2–5 mm long, or by a small leaf, bearing an umbelloid unit of (2–)3(–8) flowers. Androecious flower in bud ellipsoid to obovoid, 3–5 mm by 2.5–3 mm, the pedicel 1–7 mm by 0.3–0.6 mm, sometimes minutely bracteolate; at anthesis deeply 4–6-fid, 5–7 mm diam., the lobes reflexing; stamens ca. 45–60, 1.5–2 mm long, the anther ellipsoid, ca. 1 mm wide, comprising ca. ⅓–½ total length of the stamen, the connective rounded to apiculate, the internal receptacle surface pilose with short simple hairs. Gynoecious flower in bud ovoid-urceolate to subglobose-urceolate, 2.5–4 mm by 2.5–3.5 mm; at anthesis the orifice 0.6–0.8 mm diam., the styles 6–12, exserted for 0.5–1.5 mm, the internal receptacle surface velutinous with short simple hairs, the pedicel 1–4 mm by 0.5–1 mm. Fruiting receptacles borne on the leafy or leafless stems, in clusters of 1–20, ovoid to subglobose, 5–12 mm diam., the apex ± acuminate, externally scabrous with scattered stellate trichomes, the carpels 1–5 per receptacle, ovoid-compressed, 5–7 mm long, 4.5–5.5 mm wide, 3–4.5 mm thick, mucronate, with a longitudinal crest, the endocarp surface deeply foveate-sulcate.

Distribution. Endemic to the Mascarene Islands of Mauritius and Réunion (Figs. 22, 23).

Habitat. The species is occasional to locally common in lower montane wet and cloud forest in Réunion from ca. 500 to 1,700 m. In Mauritius, *Monimia ovalifolia* is known only from patches of cloud forest on the summits of Mts. Le Pouce, Cocotte, Lagrave, and Piton Grand Bassin (ca. 550–770 m), and also occurs in wet forest at Plaine Champagne (ca. 450 m).

MAURITIUS. BASSIN BLANC: path near Bassin Blanc, (fr), *Vaughan sub MAU 13081* (MAU). GRAND BASSIN: summit area, Piton Grand Bassin, ca. 700 m, 31 Jan. 1976 (fr), *Coode 4696* (K, 2 sheets); 18 Oct. 1978 (fl), *Lorence 1857* (MAU, MO); Chemin Cheval near Grand Bassin, 23 Jan. 1939 (fr), *Vaughan sub MAU 18546* (MAU). LE POUCE MT.: around summit, June 1860 (fl, fr), *Ayres s.n.* (K); at the upper limit of woods at the base of Mt. Pouce, 5 Sept. 1849 (fl), *Boivin s.n.* (P); (fl, fr), *Bojer s.n.* (K); base of the shoulder (fl), *Bouton s.n. in 1864–1865* (K); (fr), *Bouton s.n. in 1831* (P, 2 sheets); summit of the Pouce, highest part of the mountain (fl), *Bouton s.n.* (G-DC, n.v.; microfiche, MO); base of the shoulder (fl), *Bouton sub MAU 1307* (MAU); SE slope near the summit, 19 Nov. 1973 (fl), *Coode 4125* (K); ca. 30 m below summit on windward slope, 800 m, 14 Dec. 1978 (st), *Lorence 2145* (MO); 18 Aug. 1979 (fl), *Lorence 2910* (MO). MT. COCOTTE: mossy forest, summit, 10 June 1966 (fl), *Guého sub MAU 12175* (MAU, 2 sheets); indigenous vegetation along crest, 8 Nov. 1969 (fr), *Guého sub MAU 14130* (MAU, 2 sheets); summit, ca. 770 m, 1 Dec. 1978 (fl), *Lorence 1982* (K, MO); (fr), *Lorence 1983* (B, G, K, MAU, MO, P, REU, Z); 19 Dec. 1978 (st), *Lorence & Lecordier 2168* (MAU, MO, P); 17 Jan. 1979 (fr), *Lorence 2285* (MAU, MO); 29 Jan. 1979 (fr), *Lorence 2350* (MAU, MO); 10 Aug. 1979 (fl), *Lorence 2895* (MO); (fl), *Lorence 2896* (B, G, K, MAU, MO, P, REU, Z); 29 Jan. 1979 (st), *Lorence 2964* (MO). MT. LAGRAVE: dense thicket along crest, 27 Sept. 1969 (fl), *Guého sub MAU 14097* (MAU, 2 sheets); dense thicket on N flank, 27 Sept. 1969 (fl), *Guého sub MAU 14105* (MAU, 2 sheets); S slope facing Eau Bleue Reservoir, 620 m, 24 May 1979 (st), *Lorence & Lecordier 2650* (K, MAU, MO). PLAINE CHAMPAGNE: track from Plaine Champagne to Black River Gorges, 1,400 ft. (ca. 450 m), 4 Feb. 1975 (st),

Coode s.n. (K). WITHOUT PRECISE LOCALITY: (fl), *Ayres s.n.* (MO, 2 sheets); (fr), *Bijoux sub MAU 1308* (MAU); (fr), *Bijoux sub MAU 1309* (MAU); (fr), *Bijoux sub MAU 1310* (MAU); (fl), *Boivin s.n.* (P, 2 sheets); (fl), *Bojer s.n.* (K); (fl), *Bouton s.n. in 1829* (K); (fl), *Bouton s.n.* (P, 2 sheets); (fl), *Ilardwicke s.n.* (G); (fl), *Neraud s.n.* (G); (fl), *Schledl s.n.* (P); (fr), *Vesco s.n. in 1850* (P, 2 sheets). RÉUNION. BASSE VALLÉE: Le Grand Coudé (above St. Joseph), 1,100 m, June 1957 (fl), *Bosser 12215* (P); heights of Basse Vallée, La Coudée, 22 Nov. 1973 (st), *Coode s.n.* (K); ravine of Basse Vallée, 25 Nov. 1970 (fr), *Friedmann 753* (P); Basse Vallée near St. Philippe, 900 m, 13 July 1979 (fl), *Lorence & Cadet 2726* (MO); (fl), *Lorence & Cadet 2727* (MAU, MO); 17 May 1976 (st), *Richardson 4152* (K); 17 Feb. 1956 (st), *Severin 50* (P, REU). BOIS BLANC: above Bois Blanc, 800 m, 8 Aug. 1972 (fl), *Cadet 3721* (REU); 800 m, Apr. 1972 (fl), *Friedmann 1884* (P). BÉBOUR FOREST: Bébour Peak (Piton Rond de Bébour), 1,300–1,600 m, 23 Feb. 1979 (fr), *Lorence & Cadet 2430* (MAU, MO); region of Bébour near Pl. des Palmistes, 19 Jan. 1975 (fr), *Bernardi 15171* (P). GRAND ÉTANG: 500 m, 15 July 1979 (fl), *Lorence & Rolland 2754* (MO); (fl), *Lorence & Rolland 2755* (MAU, MO); (fl), *Lorence & Rolland 2756* (MAU, MO); (fl), *Lorence & Rolland 2757* (MAU, MO). LANGEVIN: high valley of Langevin, 1,500 m, 10 May 1976 (fl), *Cadet 5400* (REU); valley to Langevin below Plaine des Sables, 1,400 m, 10 May 1976 (fl, fr), *Richardson 4106* (K). MORNE DES PATATES À DURAND: 1,200 m, Mar. 1973 (fr), *Friedmann 2199* (P). PLAINE DES CAFRES: bank of Rivière des Remparts, 1948 (fl), *Anon. s.n.* (probably *Rivals*) (TL-R); Grand Bassin at base of Piton Bleu, 11–12 July 1943 (fr), *Rivals s.n.* (TL-R); Grand Montée of the Plaine des Cafres, 1,300–1,500 m, 12 July 1943 (fl), *Rivals s.n.* (TL-R); Bank of Rivière des Remparts, Vallon Hoarau, 20 Oct. 1948 (fl), *Rivals s.n.* (TL-R). PLAINE DES PALMISTES: high plateaux, (fl, fr), *Cordemoy s.n.* (TL-R); Grande Montée, 1,400 m, roadside, 20 Dec. 1942 (fl, fr), *Rivals s.n.* (TL-R); (fr), *Rivals s.n.* (TL-R); Petite Plaine above Plaine des Palmistes, 1,200 m, 25 Feb. 1979 (fr), *Lorence & Rolland 2452* (MAU, MO). RIVIÈRE DES REMPARTS: Roches Plates path, 5,400 ft. (ca. 1,800 m), 20 Nov. 1968 (fl), *Barclay 1273* (K, MAU); high valley of Rivière des Remparts, 1,700 m, 20 Nov. 1968 (fl), *Cadet 1726* (REU); 1,650 m, 7 Mar. 1975 (fl), *Cadet 5106* (REU). ST. PHILIPPE (VICINITY): Mare Longue forest, 500 m, 25 Feb. 1975 (fr), *Cadet 5082* (REU); 1–2 Feb. 1968 (fr), *Capuron 28182-SF* (P, 2 sheets); 23 Nov. 1973 (fr), *Coode et al. 4176* (K, 2 sheets; MAU, REU); 25 Feb. 1975 (fr), *Coode 4954* (K, 2 sheets; REU); 2 Mar. 1979 (fr), *Lorence, Lorence & Cadet 2482* (MAU, MO); Mare d'Arzule, 500 m, Apr. 1944 (fr), *Rivals s.n.* (TL-R). TAKAMAKA: path from Takamaka towards Ilet à Bananes, 2,500 ft. (ca. 800 m), 18 Feb. 1968 (fr), *Barclay 1240* (K, MAU); rain forest, Tacamaca, 21 Dec. 1971 (fr), *Bosser 20926* (P); Takamaka forest, Ilet à Bananes, ca. 800–900 m, 10 Mar. 1979 (fr), *Lorence & Rolland 2531* (MO); ca. 1,000 m, 8 May 1976 (st), *Richardson et al. 4100* (K, MO). WITHOUT PRECISE LOCALITY: (fl), *Anon. ex Herb. Ventenat s.n.* (G); (st), *Anon. s.n.* (probably *Cordemoy*) (TL-R); (fl), *Frappier 269* (P); (fr), *Frappier 270* (P); (fl), *Frappier 271* (P). LOCALITY (ISLAND) UNKNOWN: (fl), *Anon. ex Herb. Richard 66* (P); (fl), *Anon. ex Herb. Richard s.n.* (P); (st), *Anon. sub Herb, Willd. 18080* (B, n.v.; microfiche, MO); "Madagascar" (probably Mauritius) (fl), *Colebrooke s.n.* (G); "Rodrigues" (probably Réunion) (fr), *Balfour s.n. in Aug.–Dec. 1874* (K).

Monimia ovalifolia differs from *M. amplexicaulis* and *M. rotundifolia* in having much sparser and uniquely short stellate-peltate laminar trichomes with the arms united basally for ca. ⅓–½ their length (Fig. 9D, E), flowers with much smaller receptacles, and in having tanniferous idioblasts in the petiolar cortex. Although characterized by a generally lower altitudinal range, *M. ovalifolia* occurs sympatrically with *M. rotundifolia* in many localities in Réunion (e.g., at Bébour), where both species remain distinct, apparently by temporal isolation of flowering.

Populations of *Monimia ovalifolia* from Réunion tend to have fewer simple and fasciculate trichomes on the stem, petiole, costa, and inflorescence. The leaves are larger than in Mauritius plants and more variable in shape, often obtuse or even orbiculate. Furthermore, crushed leaves of the Réunion plants usually produce a faint, citron-like odor not apparent in Mauritian plants, even though ethereal oil cells are present in the mesophyll of both. Intergradation of plants from the two islands is total, however, and formal recognition of infraspecific variants is impossible.

Vernacular name. Mapou (Réunion).

EXCLUDED SPECIES

Monimia lastelliana Baill., Bull. Mens. Soc. Linn. (Paris) 1: 342. 1882; Perk. & Gilg, Pflanzenr. 4, 101: 65. 1901. [= *Tambourissa lastelliana* (Baill.) Drake, see discussion under this species].

Decarydendron Danguy, Bull. Mus. Hist. Nat. (Paris), Ser. 1, 34: 279. 1928; Cavaco, Bull. Soc. Bot. France 105: 38. 1958; Cavaco, Blumea Suppl. 4: 28, fig. 1. 1958; Cavaco in Humbert, Fl. Madagascar 80: 8, fig. II:1–8. 1959. TYPE: *D. helenae* Danguy.

Monoecious treelets or small trees 4–8 m tall, the trunk sometimes swollen basally, the new growth velutinous to canescent, the hairs simple or in fascicles of 2. Leaves opposite, petiolate, adaxially glabrescent, abaxially ± pubescent especially along costa and major veins, the venation festooned brochidodromous, the margin serrate to dentate; juvenile and sucker leaves unknown. Inflorescence cauliflorous, sometimes produced at the swollen base of the trunk, or

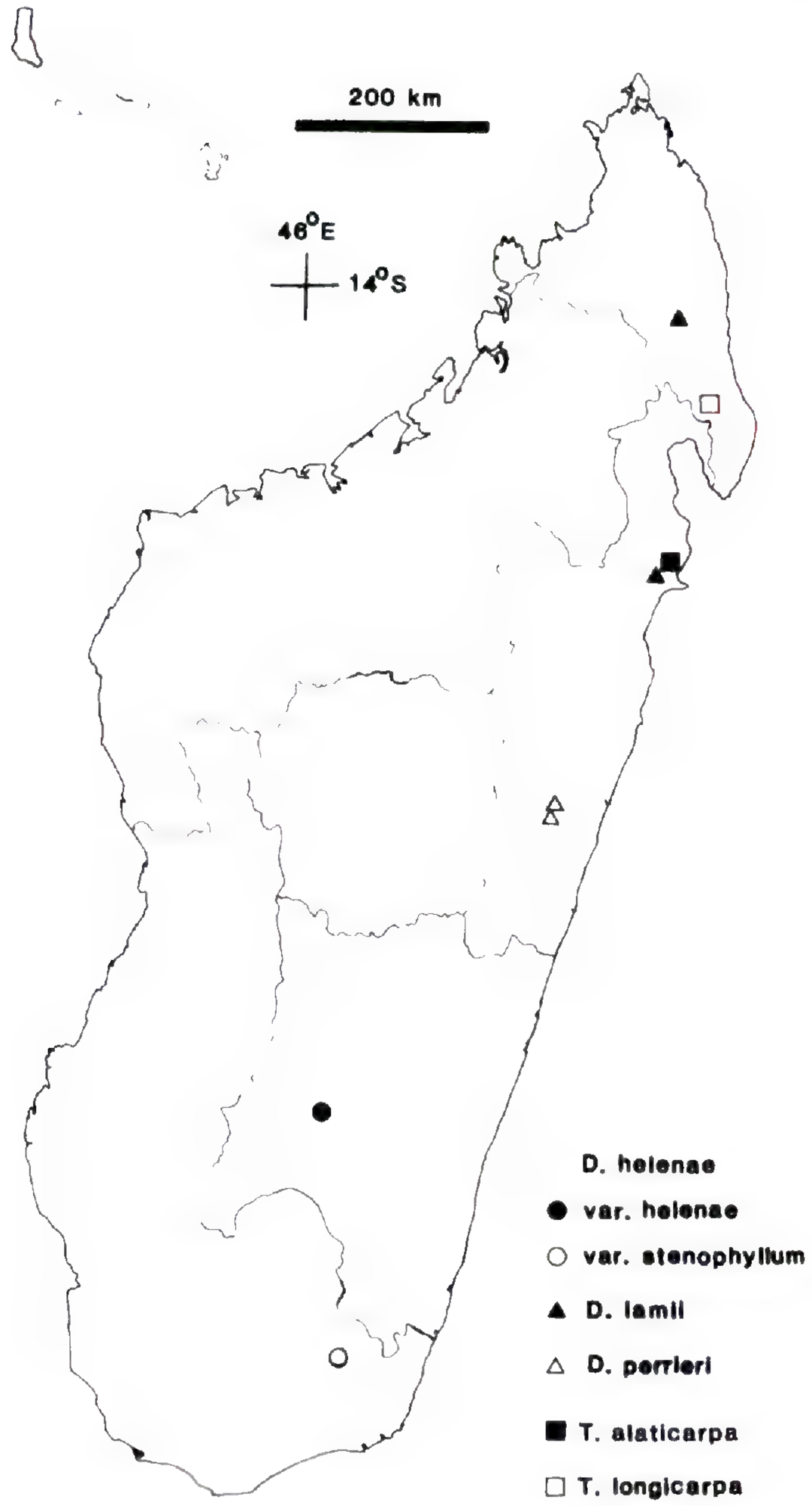


FIGURE 24. Distribution map of *Decarydendron* and two species of *Tambourissa* in Madagascar.

ramiflorous, a short, pubescent unisexual or sexually mixed pleiochasium of 5–15 flowers, often terminated by a gynoecious flower, the pedicels short, bracteolate. Androecious flower in bud subglobose to napiform, pubescent, the tepals imbricate, opening gradually, not splitting, at anthesis shallowly cupuliform to hemispherical, the rim bearing 10–15 large, subequal, broadly obtuse, radially arranged tepals in 1–2 series; stamens eglandular, 16–60, situated on the ± glabrous inner receptacle surface, the filament slender, distinct, the anther ovoid-ellipsoid, tetrasporangiate, the 2 loculi lateral, separate, longitudinally dehiscent, extrorse, the connective small, scarcely or not prolonged; pollen inaperturate, spheroid to subovoid, the sexine corrugate to rugulate, the sexinous elements short, finger-like. Gynoecious floral receptacle subglobose in bud, expanding gradually, not splitting, at anthesis broadly obconical to turbinate, ± angular, the walls fleshy, the rim bearing 9–15 broadly obtuse, radially arranged tepals, often eventually caducous, the carpels numerous, ca. 300–1,000, free, lining the receptacle, subsessile, clavate, ca. 1.5–2 mm long, ± polyhedral, the small stylar canal situated laterally in the basal half, the solitary ovary unilocular, the small loculus confined to the base of the carpel, containing a single pendulous, anatropous ovule, the carpels interspersed with ± dense, short simple hairs. Fruiting receptacle, mature carpels, and chromosome number unknown.

The genus was named after the French botanical explorer, R. Decary, who collected in Madagascar during the early part of the twentieth century.

Distribution. The three described species of *Decarydendron* are endemic to the wet evergreen forest zones of central and eastern Madagascar (Fig. 24).

TAXONOMIC HISTORY OF *DECARYDENDRON*

The genus *Decarydendron* was described by Danguy (1928) based on the species *D. helenae.* Thirty years later Cavaco (1958a, 1958b), described two additional species, *D. perrieri* and *D. lamii,* as well as another variety of *D. helenae,* var. *stenophyllum,* in preparation for his treatment for the "Flore de Madagascar" (1959). Herbarium material is scarce, and many additional flowering and fruiting collections and field observations are required for a meaningful revision of the genus.

SYSTEMATIC POSITION OF *DECARYDENDRON*

Decarydendron possesses the greatest constellation of primitive characters of any of the Malagasy Monimiaceae genera, notably the broad, shallowly concave floral receptacles with many large, whorled imbricate tepals, the numerous free, subsessile clavate carpels, and the cupuliform androecious flowers which expand gradually without splitting into segments as in the other genera (Fig. 14E). These features readily distinguish *Decarydendron* from the other two Madagascan genera which form an increasingly specialized series. *Decarydendron* resembles *Hedycarya* from Oceania in a number of respects, including the gynoecious floral morphology. Its mature fruiting receptacle presumably resembles

that of the latter genus in having numerous sessile carpels situated on a flat, discoid receptacle.

Money et al. (1950) placed *Decarydendron* in the subfamily Monimioideae with the other Madagascan genera. Hutchinson (1964) placed it in the tribe Hedycaryeae within the same subfamily on the basis of its free, sessile carpels. In redefining the Monimioideae to include only *Monimia* and *Peumus,* Thorne (1974) created a new subfamily, the Mollinedioideae, to house the remaining genera formerly included in the Monimioideae. *Decarydendron* is therefore now included in the Mollinedioideae. As its pollen and vegetative and floral anatomy correspond most closely with the other members of this subfamily, I agree with its placement there.

KEY TO THE SPECIES OF *DECARYDENDRON*

1a. Leaves abaxially velutinous; petioles 3–5 mm long; tepals of androecious flowers crenulate ..... 1. *D. perrieri*

1b. Leaves abaxially glabrate or at most puberulent; petioles 10–20 mm long; tepals of androecious flowers entire, not crenulate.

2a. Laminar teeth 2–4 mm long; androecious flowers with 40–60 stamens ..... 2. *D. helenae*

2b. Laminar teeth 0.5 mm long; androecious flowers with 16–26 stamens ..... 3. *D. lamii*

1. Decarydendron perrieri Cavaco, Bull. Soc. Bot. France 105: 38. 1958; Cavaco in Humbert, Fl. Madagascar 80: 9, fig. II:6–8. 1959. TYPE: Madagascar. Tamatave: Analamazaotra forest (near Perinet) (fl), *Perrier de la Bâthie 10089* (holotype, P).

Monoecious treelet or small tree 5–8 m tall, the base of the trunk swollen, the new growth densely velutinous, the mature leafy stems tomentose. Leaves opposite to subopposite, petiolate; petioles sparsely tomentose, 3–5 mm by 1.5–2 mm; lamina sparsely tomentose adaxially, velutinous abaxially, chartaceous, narrowly elliptic to narrowly ovate, 80–165 mm by 35–65 mm, the apex acuminate, the base broadly cuneate to obtuse, the secondary veins 5–7 pairs, making a 55–65° angle with the costa, depressed adaxially, the venation visible to 3° adaxially, to 4° abaxially, finely reticulate, prominent, the margin serrate-dentate with 30–35 pairs of subequal, acuminate teeth 1–3 mm long. Inflorescence cauliflorous at the swollen base of the trunk, sometimes extending up the trunk for some distance, a velutinous pleiochasium of 5–7 flowers, either unisexual of androecious flowers or sexually mixed and terminated by a gynoecious flower, the floral axis 120–220 mm by 3–4 mm, the pedicels 5–17 mm by 1.5–3 mm, basally bracteolate. Androecious flowers smaller than the gynoecious, the receptacle thick, externally velutinous, cupuliform, 7–14 mm diam., the margin bearing 10–18 subequal thick, deltoid-ovate or suborbicular tepals 5–6 mm long by 4–5 mm wide in two series, the external ones crenulate, the internal ones sinuate; stamens ca. 25, glabrous, 2–3 mm long, ellipsoid, the filament short, not prolonged, the anther ovoid, occupying ⅔ total length of the stamen. Gynoecious flower at anthesis externally velutinous, cupuliform, thick, 14–17 mm diam., with two longitudinal external ridges, each terminated by an ovate-acuminate, denticulate bracteole, the tepals subequal, deltoid to ovate, 3–6 mm by 5–7 mm, numbering 12–15, in two whorled series, the outer ones externally velutinous, the inner ones glabrate; carpels numerous, ca. 800–1,000, lining the receptacle, free, clavate, ca. 1.5 mm long. Fruiting receptacle unknown.

Distribution. Endemic to Madagascar (Fig. 24).

Habitat. The species is known only from the type locality, where it occurs in *Tambourissa/Weinmannia* wet forest at ca. 900 m.

MADAGASCAR. TAMATAVE: Perinet forest, 900 m, 30 Mar. 1974 (fl), *Cremers 3017* (MAD).

In addition to the characters cited in the key, *Decarydendron perrieri* differs from its congeners by the presence of a series of smaller tepals alternate with the larger outer series in the female flowers. Further collections, including fruiting material, and field observations are required to further assess its affinities within the genus.

2. Decarydendron helenae Danguy, Bull. Mus. Nat. Hist. (Paris), Ser. 1, 34: 279. 1928; Cavaco in Humbert, Fl. Madagascar 80: 10. 1959. TYPE: Madagascar. Fianarantsoa: forest at N base of Ivohibé Peak, 20 Sept. 1926 (fl), *Decary 5391* (holotype, P).

Small monoecious tree 7 m tall and 25 cm diam., the new growth golden tomentose, the mature leafy stems glabrescent, the trichomes simple or in fascicles of 2. Leaves opposite, petiolate; petioles 10–18 mm by 1.5–2.5 mm, glabrate; lamina ovate-elliptic to narrowly obovate-elliptic, 150–200 mm by 50–130 mm, chartaceous, adaxially hirsutulous when young,

glabrescent, abaxially hirsutulous, velutinous along the costa and veins, the apex acute to shortly and abruptly acuminate, the base narrowly cuneate to obtuse, the secondary veins 5–8 pairs, making a 50–70° angle with the costa, the venation visible to 3° adaxially, to 4° abaxially, the margin prominently serrate-dentate, the teeth 15–25 pairs, unequal, acute to acuminate, 2–4 mm long, the glandular tips indurated. Inflorescence probably cauli- or ramiflorous, a finely velutinous pleiochasium of 5–7 flowers, unisexual of androecious flowers, or sexually mixed and terminated by a gynoecious flower, the floral axis 130–230 mm by 3–4 mm, the pedicels 10–15 mm by 1–1.5 mm, flattened near the junction with the receptacle, basally bracteolate. Androecious flower at anthesis cupuliform to hemispherical, 12–25 mm diam., the margin bearing a single series of 7–15 unequal, obtuse tepals 3–8 mm long by 6–10 mm wide, pilose on both surfaces; stamens ca. 40–60, glabrous, ellipsoid, 3–4.5 mm long, the filament ca. 0.5 mm long, the connective thick, not prolonged, the anther 2.5–4 mm long. Gynoecious flower larger than the androecious, at anthesis the receptacle broadly obconic to cupuliform, 15–35 mm long by 20–40 mm wide, externally pilose-velutinous, the margin bearing a single series of 8–15 thick, obtuse tepals 2–5 mm long by 2–4 mm wide; carpels numerous, up to 300 or more, lining the receptacle, clavate, 1.5–2.5 mm long, glabrous, interspersed with numerous short, simple trichomes. Fruiting receptacle and mature carpels unknown.

Distribution. Endemic to Madagascar (Fig. 24).

Decarydendron helenae differs from its congeners in having a combination of adaxially glabrate or only sparsely puberulent leaves with large marginal teeth, and more numerous stamens (up to 60 per flower). The species, particularly the variety *stenophyllum*, appears to be most closely allied to *D. perrieri*. More numerous collections and field studies are required to critically assess its status.

KEY TO THE VARIETIES OF *DECARYDENDRON HELENAE*

1a. Leaves 90–130 mm wide; tepals ca. 15 ..... 2a. var. *helenae*

1b. Leaves 50–75 mm wide; tepals 7–10 ..... 2b. var. *stenophyllum*

2a. Decarydendron helenae var. **helenae.**

Variety *helenae* differs primarily in having larger leaves, a more robust inflorescence, and larger flowers than var. *stenophyllum*. Also, its receptacle lacks the two lateral ridges present in the latter variety. It was named after Helen Decary, who assisted her husband in his botanical research.

Habitat. Known only from the type, which was collected at the base of Ivohibé Peak in the Andringitra Massif in southern central Madagascar, it probably occurs in montane evergreen wet forest, most likely in the upper limits of the *Tambourissa/Weinmannia* zone (Fig. 24).

2b. Decarydendron helenae var. **stenophyllum** Cavaco, Bull. Soc. Bot. France 105: 39. 1958; Cavaco in Humbert, Fl. Madagascar 80: 10. 1959. TYPE: Madagascar. Tulear: upper basin of the Mandrare River (SE), pass and summit of Marosoui, 1,000–1,400 m, forest on gneissic laterite, 14–15 Nov. 1928 (fl), *Humbert 6613* (holotype, P; isotypes, K, MAD, US).

In addition to its narrower leaves, variety *stenophyllum* has a less robust inflorescence, smaller flowers with fewer tepals, and floral receptacles with two prominent, lateral ridges ending in small bracteoles. Whether these differences are constant or merely represent stages within a range of variation can only be ascertained by additional collections and field studies. The only known (type) collections of the varieties are, however, geographically separated by about 250 km.

Distribution. Endemic to Madagascar (Fig. 24).

Habitat. Variety *stenophyllum* is known only from the southeastern part of Madagascar, probably in the *Tambourissa/Weinmannia* wet forest zone.

3. Decarydendron lamii Cavaco, Blumea Suppl. 4: 28, fig. 1. 1958; Cavaco in Humbert, Fl. Madagascar 80: 12, fig. II:1–5. 1959. TYPE: Madagascar. Tamatave: Soanierana-Andasibé, 10 Dec. 1938 (fl), *Lam & Meeuse 5835* (holotype, presumably BO, n.v., photo, P; isotype, P).

Small monoecious understory tree 5 m tall, the new growth fulvous-velutinous, the mature

leafy stems villous, 3–5 mm diam. Leaves opposite, petiolate; petioles 10–20 mm by 1.5–2 mm, velutinous; lamina chartaceous, narrowly elliptic to narrowly obovate-elliptic, 100–190 mm by 40–72 mm, the apex abruptly short acuminate, the base cuneate, the adaxial surface glabrate, the abaxial surface appressed pilose, especially on the costa and veins, the secondary veins 10–12 pairs, making a 65–75° angle with the costa, raised on both surfaces, the venation visible to 3° adaxially and to 4° abaxially, the margin plane, finely dentate, the teeth 40–50 pairs, 0.5 mm long, glandular tipped. Inflorescence cauliflorous from meristematic swellings on the trunk or ramiflorous, a pleiochasium of 8–15 flowers, unisexual of androecious flowers or sexually mixed and terminated by a single gynoecious flower, the floral axis 100–220 mm by 2 mm, densely fulvous-velutinous. Androecious flowers smaller than the gynoecious, at anthesis shallowly cupuliform to disciform, open, 12–16 mm diam. by 5–8 mm long, externally finely strigose-sericeous, the margin bearing 10–12 entire, obtuse, ovate to ligulate tepals 2–3 mm wide and long, in two series, the pedicel 6–25 mm by 1 mm, basally bracteolate, the bracteole to 4 mm long; stamens 16–26, ellipsoid to obovoid, 1.8–3 mm long by 1.5–1.8 mm wide, the filament distinct, short, the anther occupying ⅔–¾ total length of the stamen, the connective thick, not prolonged, the internal receptacle surface glabrous, purple. Gynoecious flower at anthesis obconical, 30 mm diam. by 24 mm long, externally finely velutinous, the carpels numerous (probably ca. 500 or more), lining the receptacle. Fruiting receptacle and mature carpels unknown.

Distribution. Endemic to Madagascar (Fig. 24).

Habitat. The species is known from the lower montane wet forest zone of Myristicaceae/*Anthostema* in the eastern region, below 900 m.

MADAGASCAR. DIEGO SUAREZ: S slope of Betsomanga, Bassin of Androranga River, 700 m, 18 Nov. 1950 (fl), *Capuron 827-SF* (P). TAMATAVE: Andapa District, eastern slopes of the Marojejy Massif, Lokoho River basin, E of Ambalamansy II, 450–800 m, rain forest on gneissic laterite, 28 Nov. 1948 (st), *Humbert & Capuron 22154* (MO).

In addition to the characters cited in the key, *Decarydendron lamii* differs from its congeners in that the androecious flowers are purple within. Like the other species in the genus, it is poorly known.

Ephippiandra Decne., Ann. Sci. Nat. (Paris), Ser. 4, 9: 278, pl. 7. 1858; A.DC., Prodr. 16(2): 662. 1868; Baill., Hist. Pl. ed. 1, 1: 304. 1869; Perk., Engl. Bot. Jahrb. 25(4–5): 551, t. 5: 1–5. 1898; Perk. & Gilg, Pflanzenr. 4, 101: 50, fig. 9. 1901; Perk., Pflanzenr. 4, 101 (Nachtr.): 15. 1911; Perk., Gatt. Monim. 32, fig. 19. 1925; Cavaco, Bull. Soc. Bot. France 104: 610. 1957; Cavaco in Humbert, Fl. Madagascar 80: 4. 1959; Hutch., Gen. Fl. Pl. 1: 117. 1964. TYPE: *E. myrtoidea* Decne.

Hedycaryopsis Danguy, Bull. Mus. Hist. Nat. (Paris), Ser. 1, 34: 278. 1928, synon. nov. TYPE: *H. madagascariensis* Danguy.

Monoecious shrubs, treelets or trees 10–25 m tall, the trunk attaining 50 cm diam., the new growth pubescent to glabrate, the hairs simple. Leaves opposite to subopposite, petiolate, subglabrous or ± pubescent abaxially, especially along the costa and veins, the venation festooned brochidodromous, semicraspedodromous or craspedodromous, the margin entire or sparsely dentate apically with acute, glandular teeth, or sinuate-dentate with rounded, apically depressed glandular teeth; juvenile and sucker leaves unknown. Inflorescence axillary, terminal, or ramiflorous on leafless stems, a short, 5-flowered unisexual pleiochasium or a 3–5-flowered sexually mixed dichasium, the gynoecious flower solitary and terminal, maturing first, the androecious flowers lateral, or the flowers solitary and axillary, the pedicels ± long and slender, basally bracteolate. Androecious flower in bud globose to ellipsoid, bearing 2–4(–5) small tepals apically, at anthesis splitting deeply into 4(–5) ± regular valvate segments, these spreading flat or reflexing, the apex often bearing 1–2 obtuse, scale-like tepals internally; stamens eglandular, ca. 9–50, situated irregularly or in several series on the glabrous to puberulent internal receptacle surface, ligulate to shortly deltoid, the filament broad, short or sessile, the anther tetrasporangiate, the 2 loculi lateral and separate or connivent or confluent apically, longitudinally dehiscent, extrorse; pollen inaperturate, spheroid to ovoid, the exine thick, the sexine granulate with few to many, small to large scattered verrucae or gemmae. Gynoecious flower in bud subglobose-discoid, concave, the margin usually bearing 4–8(–16) small, decussate deltoid tepals; at anthesis expanding gradually, not splitting, broadly obconic to discoid, the torus flat to concave, bearing ca.

15–120 free, short sessile, 4–6-sided columnar carpels ca. 1–1.5 mm long, the apex flat, the small stylar canal lateral, medial, the ovary unilocular, the solitary ovule anatropous, situated in a small locule near the base of the carpel, the carpels interspersed with short, simple hairs. Fruiting receptacle discoid, enlarged, fleshy and red when fresh, the flat to convex surface bearing ca. 10–75 free carpels, each surrounded basally by a cupule for ⅓–½ its length; mature carpels ovoid to ellipsoid, 7–12 mm long, the thin fleshy mesocarp ripening black, the endocarp thin, horny, pale brown, the surface scrobiculate, the endosperm fleshy. Chromosome number unknown.

Distribution. All six species are endemic to Madagascar (Figs. 25, 26).

Habitat. The genus ranges from lower montane wet and cloud forest to high altitude montane sclerophyllous forest and ericoid formations.

TAXONOMIC HISTORY OF *EPHIPPIANDRA*

The genus *Ephippiandra,* described by Decaisne in 1858 based on *E. myrtoidea,* was named in reference to the low, saddle-shaped anthers characteristic of the species. A second species, described by Perkins (1911) as *Tambourissa microphylla,* was subsequently transferred to *Ephippiandra* by Cavaco (1957a). In the same year Cavaco (1957c) described a third species and established two sections in the genus based on the presence (section *Staminodia*) or absence (section *Ephippiandra*) of fleshy tepals on the inner tips of the receptacle lobes, which he referred to as "staminodes."

Danguy described *Hedycaryopsis* in 1928 based on *H. madagascariensis,* and Cavaco (1958c) subsequently described three additional species preceding his treatment for "Flore de Madagascar" (1959).

GENERIC DELIMITATIONS AND SYSTEMATIC POSITION OF *EPHIPPIANDRA*

Danguy (1928) established *Hedycaryopsis* as a segregate genus primarily on the basis of its gynoecious flowers, which he felt approached those of *Hedycarya* Forst. (syn. *Carnegieodoxa* Perk.) from Oceania. The discoid to broadly obconic gynoecious flowers of *Hedycaryopsis,* like those of *Ephippiandra,* are usually bordered by several pairs of minute, decussate deltoid tepals and the torus bears few to numerous free, sessile polyhedral-columnar carpels on its surface (15–38 in *Ephippiandra*; 22–120 in *Hedycaryopsis*; Fig. 14F, G). Furthermore, carpels of both possess oblique lateral stylar canals (Fig. 13C, D). Danguy apparently never examined gynoecious flowering material of *Ephippiandra,* because he makes no mention of it in his discussion (the type of *E. myrtoidea* has only androecious flowers and fruit). Clearly, gynoecious floral morphology does not support segregation of *Hedycaryopsis* from *Ephippiandra.*

Furthermore, fruiting receptacles of both genera are morphologically identical. Mature fruiting receptacles in both consist of a fleshy, discoid torus, red when ripe, bearing few to many ovoid to ellipsoid carpels surrounded basally by cupules (Fig. 14H). Carpels of both have a thin mesocarp, green when fresh, overlying the thin, horny endocarp. Understandably, fruiting characters have never been used to distinguish the genera.

Although Danguy (1928) noted that androecious flowers of *Hedycaryopsis* scarcely differed from those of *Tambourissa,* Cavaco (1957c, 1959) felt that stamens were a stable key character separating *Ephippiandra* from *Hedycaryopsis* and *Tambourissa.* He stated that in *Ephippiandra* the stamens were sessile and broader than long ("déprimées") with the loculi apically confluent into a single, crescentiform loculus, as opposed to *Hedycaryopsis* which had separate, lateral loculi and an apically prolonged connective. He ignored, or at least failed to mention, however, that in species such as *E. myrtoidea* the loculi may be both connivent as well as confluent in the same flower. *Tambourissa* displays the entire range of conditions and the loculi may be separate, connivent, or confluent not only apically but basally as well in various species. Two or more of these conditions may occur in a single androecious flower of *T. cordifolia* (Fig. 42C–E). Other species such as *T. purpurea* possess broad, sessile stamens with a single loculus similar to those of some *Ephippiandra* species. Furthermore, the number of stamens is relatively small in both and overlaps (10–36 in *Ephippiandra*; 9–26 in *Hedycaryopsis*), as does the presence or absence of tepals on the extremities of the receptacle lobes. Androecious floral morphological characters are therefore clearly insufficient for generic segregation.

Examination of the pollen of two species each of *Ephippiandra* and *Hedycaryopsis* (Lorence, 1980; Lorence et al., 1984) has revealed that their

sexinous patterns correspond much more closely to each other than to any of the other Malagasy genera. Pollen of *E. microphylla* and *E. myrtoidea* both have thick, granulate to verrucate sexines with larger, scattered gemmae and folds occurring in the latter. In *H. perrieri* and *H. tsaratanensis* the sexine is also thick and granulate with large, dome-shaped verrucae and gemmae. Sexinous patterns in these two genera differ primarily in the size of the processes, but correspond much more closely to each other than to the remaining Malagasy genera. I do not feel that pollen supports separation of the two genera.

Cavaco (1959) further distinguished these genera on the basis of inflorescence structure: dichasial with a central gynoecious flower and lateral (rarely solitary) androecious flowers in *Hedycaryopsis* (Fig. 14F, G); solitary or pleiochasial in *Ephippiandra.* The only species supposedly having pleiochasia, *Ephippiandra capuronii,* actually belongs in *Tambourissa* (see below). Collections of *E. myrtoidea* (*Anon. sub Herb. ORSTOM 3366,* MAD; *Anon. sub Herb. Alaotra 300,* MAD) possess sexually mixed dichasia, however, thus undermining the validity of this character in separating the genera. Furthermore, an even greater range of inflorescence types occurs in the otherwise very cohesive genus *Tambourissa.*

Leaves of the various *Hedycaryopsis* species are extremely diverse and display a striking array of venation patterns (see section on Leaf Architecture). For example, leaves of the type species, *H. madagascariensis,* are highly specialized and generally characterized by open craspedodromous venation ending in sunken teeth at the sinuate-dentate margin (Fig. 6F), a pattern apparently derived from the brochidodromous condition (R. Keating, pers. comm.). In this respect, they differ strikingly from all other known Monimiaceae genera and may have influenced Danguy (1928) to describe the genus as new. Venation in two other species, *H. capuronii* (= *Ephippiandra domatiata*; Fig. 6C, D) and *H. tsaratanensis* (Fig. 6E), as well as some collections of *H. madagascariensis,* is transitional between craspedodromous and brochidodromous, thus linking it to *H. perrieri* (Fig. 6B) which has festooned brochidodromous venation typical of virtually all other genera of Monimiaceae, including *Ephippiandra myrtoidea* (Fig. 6A) and *E. microphylla.* This intergrading range of venation patterns provides another criterion for uniting the two genera.

Because there seems to be no basis for continued segregation of *Hedycaryopsis,* I propose that it be reduced to synonymy under *Ephippiandra,* which would thus encompass six species, necessitating one new name and three new combinations given below.

Among the Malagasy Monimiaceae belonging to the Mollinedioideae, *Ephippiandra* occupies a position intermediate between *Decarydendron* and *Tambourissa* in terms of floral morphological specialization. The strong androecious/gynoecious floral dimorphism, highly reduced tepals, sessile carpels enveloped basally by cupules in fruit, androecious receptacle closed in bud and splitting open at anthesis, and tendency towards short, sessile stamens with confluent loculi are all specializations over *Decarydendron.* Female floral construction in *Ephippiandra* is not so advanced as in *Tambourissa,* however, where the closed gynoecious receptacle splits partly open at anthesis and the carpels are inferior and syncarpous.

KEY TO THE SPECIES OF *EPHIPPIANDRA*

1a. Leaf margin sinuate-dentate with rounded, apically ± depressed teeth.
  2a. Abaxial laminar surface densely ferrugineous tomentose; floral pedicel 25–50 mm long, ferrugineous tomentose ..... 1. *E. tsaratanensis*
  2b. Abaxial laminar surface at most grayish or yellowish puberulent along costa and veins; floral pedicel 8–15 mm long, grayish canescent or villous ..... 2. *E. madagascariensis*
1b. Leaf margin entire or at most with 1–2 pairs of acute, deltoid teeth in apical portion.
  3a. Basal pair of secondary veins extending up to or beyond middle portion of lamina before joining next pair above; barbate domatia present abaxially in secondary vein axils ..... 3. *E. domatiata*
  3b. Basal pair of secondary veins joining next pair above before attaining middle of lamina; domatia absent abaxially in secondary vein axils.
    4a. Apex of lamina retuse, folded downward into a thickened flap ..... 4. *E. perrieri*
    4b. Apex of lamina shortly acuminate to acute or rounded, not retuse or thickened into a flap.
      5a. Inner portion of each androecious floral receptacle lobe bearing 1(–2) scale-like tepals ..... 6. *E. microphylla*
      5b. Inner portion of androecious floral receptacle lobes lacking scale-like tepals ..... 5. *E. myrtoidea*

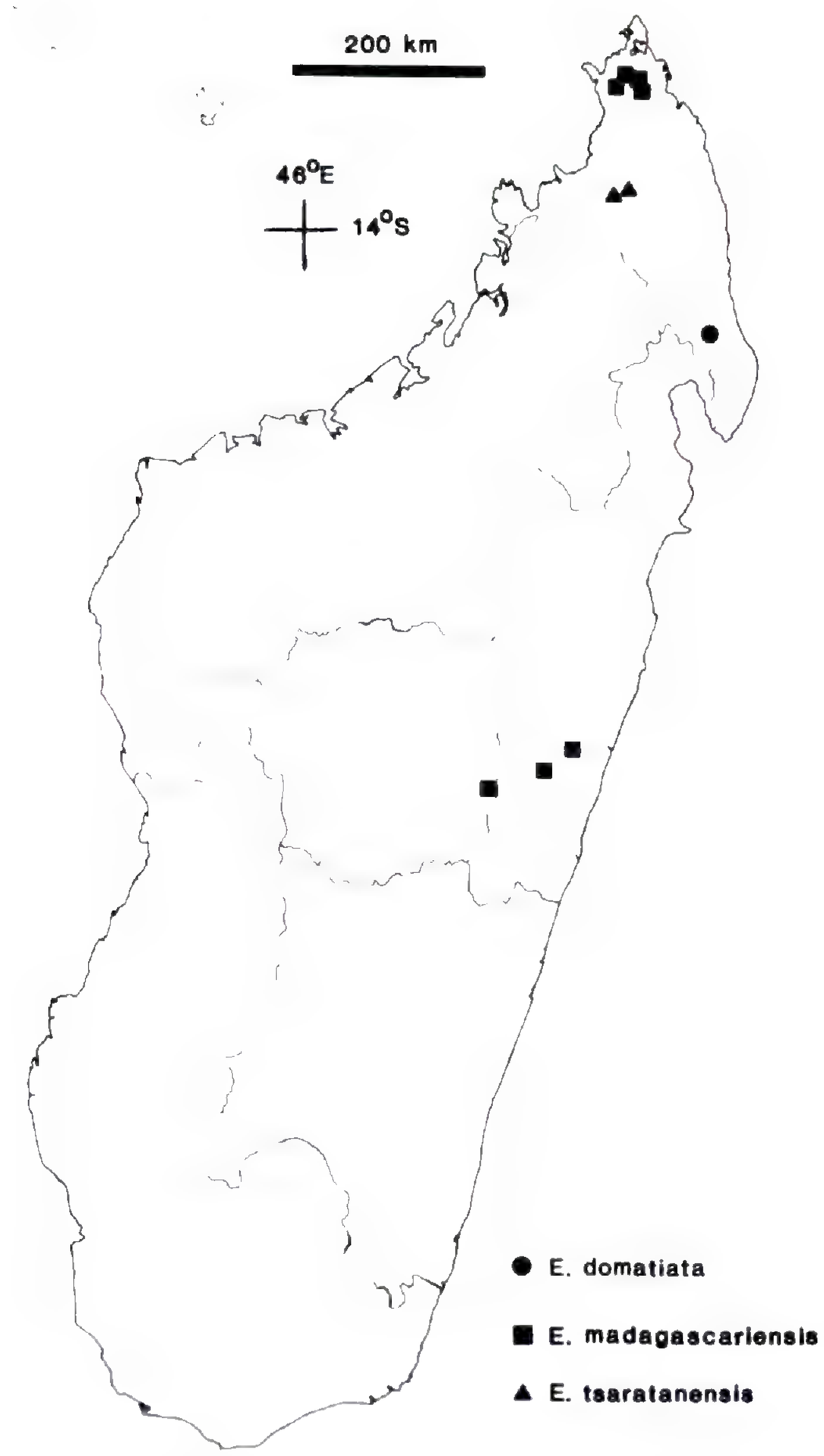


FIGURE 25. Distribution map of some *Ephippiandra* species in Madagascar.

1. Ephippiandra tsaratanensis (Cavaco) Lorence, comb. nov. *Hedycaryopsis tsaratanensis* Cavaco, Bull. Soc. Bot. France 105: 41. 1958; Cavaco in Humbert, Fl. Madagascar 80: 14, fig. III:1–5. 1959. TYPE: **Madagascar. Diego Suarez: Tsaratanana Massif, forest with herbaceous undergrowth, 1,800 m (fl), *Perrier de la Bâthie 15302*** (holotype, P).

Monecious tree 10–25 m tall, the new growth densely ferrugineous tomentose, the mature leafy stems sparsely tomentose. Leaves opposite to subopposite, petiolate; petioles 8–15 mm by 2.5–3.5 mm, ferrugineous tomentose; lamina subcoriaceous, the apex rounded, obtuse, the tip depressed, the base broadly cuneate, rounded, truncate or rarely subcordate, adaxially pubescent, glabrescent, abaxially densely ferrugineous tomentose, the secondary veins 5–8 pairs, making a 50–65° angle with the costa, the venation craspedodromous or partly brochidodromous, visible to 3° adaxially, to 4° abaxially, the margin slightly revolute, sinuate with 5–8 pairs of broadly rounded, apically depressed teeth. Inflorescence axillary, ferrugineous velutinous, a 3–5-flowered, sexually mixed dichasium, the 2–4 androecious flowers lateral, the gynoecious flower terminal and maturing first, the peduncle 15–30 mm by 2–3 mm, apically dialated, the pedicels each subtended by a linear bracteole 4–6 mm long. Androecious flower in bud ellipsoid to globose, 4–6 mm diam., ferrugineous tomentose, bearing near the apex 4 linear-ovate tepals 3–4 mm long, the pedicel 25–50 mm by 1 mm; at anthesis deeply 4-fid, 12–15 mm diam., the lobes spreading flat, each bearing a broad tepal apically within; stamens 18–20, ovate to ligulate, 2–2.5 mm long by 1–1.5 mm wide, slightly incurved, the filament thick, short or sessile, the loculi lateral, separate, occupying almost entire length of the stamen, the connective slightly prolonged, apiculate. Gynoecious flower at anthesis broadly obconical, concave, externally ferrugineous tomentose, 14–18 mm wide by 7–8 mm long, the margin bearing several minute, deltoid tepals, the pedicel 32–37 mm long; carpels 40–70, lining the receptacle, columnar, 4–5-sided, 1–1.5 mm long. Mature fruiting receptacle red when fresh, drying dark brown, irregularly discoid, convex, 60–85 mm diam., the ground tissue containing numerous stone cells, bearing (4–)40–70 free carpels surrounded basally by cupules for ⅓–½ their length, the pedicel and peduncle ca. 45 mm long by 3–4 mm diam.; mature carpels ovoid-ellipsoid, 10–12 mm long by 6–7 mm diam., green when fresh, drying brown, the mesocarp thin, fleshy, the endocarp whitish, 0.2 mm thick, the surface scrobiculate.

Distribution. Endemic to Madagascar (Fig. 25).

Habitat. The species is known only from the type locality on the Tsaratanana massif in north central Madagascar where it occurs from ca. 1,800 to 2,500 m, presumably in montane sclerophyllous cloud forest.

MADAGASCAR. DIEGO SUAREZ: Tsaratanana massif, trail up S ridge of Maromokotro, Andohanisambirano, 2,000–2,500 m; montane cloud forest, 9 May 1974 (fl, fr), *Gentry 11605* (MO).

The species is most closely allied to *Ephippiandra madagascariensis,* from which it differs

by its suborbicular, abaxially ferrugineous tomentose leaves with mixed craspedodromous/brochidodromous venation, its more densely ferrugineous tomentose parts, more robust inflorescence with longer pedicels subtended by long, linear bracteoles, and by its androecious buds bearing 4 long, linear-ovate tepals.

2. Ephippiandra madagascariensis (Danguy) Lorence, comb. nov. *Hedycaryopsis madagascariensis* Danguy, Bull. Mus. Hist. Nat. (Paris), Ser. 1, 34: 278. 1928; Cavaco in Humbert, Fl. Madagascar 80: 14, fig. IV:1–6. 1959. TYPE: Madagascar. Diego Suarez: Antsalaky forest, 700–1,000 m, 17 Oct. 1927 (fl, fr), *Ursch 66* (lectotype, P, here designated).

Monoecious tree 10–25 m tall and 50 cm diam., the new growth grayish to yellowish pubescent or canescent, the mature leafy stems 3–5 mm diam., puberulent. Leaves opposite to subopposite, petiolate; petioles puberulent, 8–15 mm by 1.5 mm; lamina subcoriaceous, ± bullate, obovate-elliptic to suborbicular, 30–90 mm by 22–60 mm, the apex obtuse, rounded, the tip retuse, the base cuneate, the adaxial surface sparsely puberulent, glabrescent, the abaxial surface puberulent, especially along the costa and veins, the secondary veins 3–5 pairs, making a 40–50° angle with the costa, depressed adaxially, prominent abaxially, dichotomizing and running into the marginal teeth, the venation craspedodromous, rarely semicraspedodromous, visible to 2° adaxially, to 3° abaxially, the margin revolute, sinuate with 2–7 pairs of broadly obtuse, apically depressed teeth. Inflorescence axillary, a sexually mixed, 3–5-flowered dichasium, the 2–4 androecious flowers lateral, subtending the terminal gynoecious flower, or the gynoecious flower rarely solitary, the peduncle grayish pubescent, 15–30 mm by 1–1.5 mm, apically dilated. Androecious flower in bud globose, 3–4 mm diam., the canescent pedicel 8–20 mm by 0.6–0.8 mm, each subtended by a naviculate bracteole 2 mm long, the apex bearing 3–4 obtuse, puberulent tepals 1–2 mm long; at anthesis deeply 4(–5)-fid, ca. 10 mm diam., the lobes spreading flat; stamens 35–50, ligulate-subulate, 1.5–2 mm long by 0.7 mm wide, the filament thick, subsessile, the loculi lateral, separate, occupying almost entire length of the stamen, the connective thick, prolonged, obtuse, the internal receptacle surface glabrous. Gynoecious flower at anthesis discoid, flat, 10–15 mm diam. by 1.5 mm thick, externally canescent, the margin bearing 8 or 16 minute, deltoid tepals 0.5 mm long, the pedicel canescent, 6–15 mm by 1.5 mm; carpels ca. 140–150, lining the receptacle, sessile, columnar, 5–6-sided, 0.8–1 mm long by 0.6–0.8 mm wide, the apex flat, interspersed with numerous short, simple hairs, the internal receptacle surface with mucilaginous secretion. Mature fruiting receptacle swollen, everted, 35–60 mm diam., bearing 30–50 carpels, the pedicel and peduncle ca. 25 mm by 3 mm; carpels ovoid-ellipsoid, 8–10 mm long by 6–7 mm diam., the basal ¼–⅓ enveloped by a cupule, the mesocarp reddish, fleshy, ca. 0.5 mm thick, the endocarp brown, foveolate-reticulate.

Distribution. Endemic to Madagascar (Fig. 25).

Habitat. Ephippiandra madagascariensis appears to be primarily restricted to the *Tambourissa/Weinmannia* wet forest zone (ca. 700–1,000 m) in northern and eastern Madagascar.

MADAGASCAR. DIEGO SUAREZ: Montagne d'Ambre, S of Les Roussettes Forestry Station by Petit Lac and above on the summit, 1,100–1,200 m, 22 Dec. 1967 (fl), *Bernardi 11977* (K, MO); Montagne d'Ambre National Park, mature wet forest, ca. 1,200 m, 23 May 1974 (fr), *Gentry 11962* (MO); Montagne d'Ambre, Dec. 1964 (st), *Morat 1182* (MAD, P); 1,100 m, 7 Dec. 1952 (st), *Schedl 170* (MAD); (st), *Schedl 177* (MAD). TAMATAVE: Beandy, Perinet, 12 Sept. 1948 (fl), *Anon. sub Service Forestier 1596-SF* (MAD); Analamazaotra forest (Perinet), 1919 (fr), *Thouvenot s.n.* (P, syntype of *Hedycaryopsis madagascariensis*); road from Anosibé to Moramanga, 9 May 1969 (st), *Anon. sub Service Forestier 26852-SF* (MO, P). TANANARIVE: Ahimiadana Canton, Andramasina, forest SE of Lake Tsiazompaniry, May 1961 (fl), *Capuron 20278-SF* (MO).

The species is most closely allied to *Ephippiandra tsaratanensis,* differing by its obovate, abaxially glabrous or sparsely puberulent leaves with open dichotomous, craspedodromous (rarely partly brochidodromous) venation, its yellowish to grayish canescent pubescence, and less robust inflorescence with shorter pedicels, bracteoles, and androecious tepals. It yields a yellowish wood said to be good for construction.

Vernacular names. Ambora, Amborabé, Tambonaika (Madagascar).

3. Ephippiandra domatiata Lorence, nom. nov. *Hedycaryopsis capuronii* Cavaco, Bull. Soc. Bot. France 105: 40. 1958; Cavaco in Hum-

bert, Fl. Madagascar 80: 13. 1959 non *Ephippiandra capuronii* Cavaco, Bull. Soc. Bot. France 104: 610. 1957. TYPE: Madagascar. Diego Suarez: Beanjada Massif (N of the Masoala Peninsula), ridge at ca. 1,100 m, 30 Dec. 1953 (fl), *Capuron 8828-SF* (holotype, P).

Monoecious shrub, the new growth with sparse, scattered hairs, glabrescent, the mature leafy stems 1–2 mm diam., becoming lenticellate. Leaves opposite, petiolate; petioles glabrous, 6–10 mm by 0.7–1 mm; lamina glabrous, chartaceous, obovate-elliptic to rhombic, 25–40 mm by 14–25 mm, the apex obtuse to retuse, often apiculate, the base cuneate, the secondary veins 2–3 pairs, the strong basal pair making a 40–45° angle with the costa, attaining top half of the lamina before uniting brochidodromously with the next pair, adaxially depressed, abaxially prominent, the axils of the basal veins domatiate and barbate abaxially, the venation visible to 2° adaxially and to 3–4° abaxially, the margin revolute, with 1–2(–3) pairs of minute teeth in the apical ½–⅓. Inflorescence axillary, a 3-flowered dichasium, the terminal gynoecious flower subtended by 2 androecious flowers, or the male flowers solitary or in cymes of 3, the peduncle glabrous, (4–)12–15 mm by 0.5 mm, with 2 basal bracteoles. Androecious flower in bud globose, 2.5–3 mm diam., glabrous, the apex with 2 pairs of broadly obtuse tepals 1.5–2 mm wide, the pedicel 7–8 mm by 0.5 mm, subtended by a bracteole 1–1.5 mm long; at anthesis deeply 4-fid, 5–6 mm diam., the lobes spreading flat, each bearing apically 2 thin, broadly obtuse tepals internally; stamens 9–10, ovoid-subulate, 1–1.5 mm long by 0.6–0.8 mm wide, the filament short, distinct, the loculi lateral, separate, occupying ca. ¾ total length of the stamen, the connective slightly prolonged, apiculate. Gynoecious flower at anthesis discoid, flat, 4.5–5 mm diam. by 1.5 mm thick, externally with a few scattered hairs, the margin entire or with a few minute, deltoid teeth, the pedicel glabrous, 9–19 mm by 0.5 mm, occasionally basally bracteolate; carpels 24–25, sessile, columnar, 0.8 mm long by 0.6–0.7 mm wide, 5–6-angled, interspersed with tufts of short, simple hairs. Fruiting receptacle unknown.

Distribution. Endemic to Madagascar (Fig. 25).

Habitat. The species is known only from the type locality, presumably in *Tambourissa/Weinmannia* wet forest at ca. 1,100 m.

Ephippiandra domatiata is readily distinguishable from its congeners by its glabrous inflorescence and stems, and particularly by its leaves with abaxially domatiate, barbate secondary vein axils. Further collections, especially fruiting material, and field observations are greatly desired.

4. Ephippiandra perrieri (Cavaco) Lorence, comb. nov. *Hedycaryopsis perrieri* Cavaco, Bull. Soc. Bot. France 105: 40. 1958; Cavaco in Humbert, Fl. Madagascar 80: 16. 1959. TYPE: Madagascar. Diego Suarez: Tsaratanana massif, forest with herbaceous understory, 2,000 m, Apr. 1929 (fl, fr), *Perrier de la Bâthie 16249* (holotype, P).

Monoecious shrub, treelet or tree 12–15 m tall, the new growth finely cinereous pubescent, the mature leafy stems 2–3 mm diam., grayish puberulent, glabrescent, often with large, elliptic lenticels. Leaves opposite to subopposite, petiolate; petioles 5–11 mm by 1 mm, finely puberulent, glabrescent; lamina chartaceous to subcoriaceous, glabrous, elliptic to obovate or obcordate, 25–55 mm by 15–35 mm, the apex obtuse, rounded, the tip retuse or emarginate, folded under into a thickened flap, the base narrowly cuneate, the secondary veins 3–4 pairs, making a 45–55° angle with the costa, obscure adaxially, prominent abaxially, the venation visible to 3° adaxially and to 4° abaxially, the margin entire, ± revolute. Inflorescence axillary, a 3-flowered, sexually mixed dichasium, the gynoecious flower terminal, subtended by a pair of androecious flowers, or the androecious flowers solitary, axillary, the peduncle 10–15 mm by 1 mm, finely puberulent, subtended by several small, deltoid bracteoles. Androecious flower in bud globose, 3 mm diam., with scattered appressed hairs, the apex bearing 2 obtuse to subulate, ciliate tepals 1–1.5 mm long, the pedicel 8–20 mm by 0.7 mm, often with 1–2 minute bracteoles; at anthesis deeply 4–5-fid, 9–10 mm diam., the lobes spreading flat or recurving slightly, internally glabrous, each terminated by a broad, retuse or bifid tepal internally; stamens 15–20, recurved, 2–2.5 mm long, the filament slender, 1–1.5 mm long, the anther ovoid-ellipsoid, 1 mm long, the loculi lateral, separate, the connective prolonged, apiculate. Gynoecious flower on a pedicel 12–20 mm by 1 mm, bracteolate basally or medially, the receptacle open in bud; at anthesis flat, discoid, 4–6 mm diam. by 2 mm thick,

externally finely gray sericeous, the margin bearing 4–8(–16) minute, deltoid tepals ca. 0.5 mm long; carpels 20–25, bluntly columnar, 1 mm long by 0.6–0.8 mm wide, 5–6-angled, covering the torus, interspersed with short, simple hairs. Mature fruiting receptacle swollen, 15–20 mm diam., usually with 2–4 carpels, the pedicel and peduncle 25–45 mm by 1.5 mm; carpels ovoid, 8–9 mm by 6–7 mm, the basal ¼–⅓ enclosed by a raised cupule, the mesocarp thin, fleshy, the endocarp light brown, striate-reticulate.

Distribution. Endemic to Madagascar (Fig. 26).

Habitat. The species is restricted to sclerophyllous montane cloud forest and ericoid formations on Madagascar's highest mountains, the Marojejy and Tsaratanana massifs, from ca. 2,000 to 2,650 m.

MADAGASCAR. DIEGO SUAREZ: Marojezy (Marojejy) massif, summit, 29 Mar. 1949 (fl, fr), *Anon. sub Herb Alaotra 3479* (MAD, 3 sheets); Marojejy Natural Reserve, sclerophyllous forest, 2,000 m, 27 Nov. 1972 (fl), *Guillaumet 4058* (MAD); ericoid scrub on the summit of Marojejy, 2,000–2,137 m, Dec. 1972 (fl), *Morat 4035* (MAD, P); Tsaratanana massif, 2,200–2,650 m, Nov. 1966 (fl), *Capuron 25000-SF* (MO, P); 2,100 m, Nov. 1966 (fr), *Morat 2268* (MAD, P); Andohanisambirano, 2,500 m, Nov. 1966 (fl), *Morat 2332* (MAD); (fr), *Morat 2333* (MAD).

Ephippiandra perrieri most closely resembles *E. domatiata,* but its leaves have entire margins, a more deeply retuse or emarginate apex which is thickened and folded under into a flap, lack domatia, and the inflorescence is sparsely pubescent. In sheltered forest *E. perrieri* becomes a tree, but takes on a shrubby habit on exposed slopes.

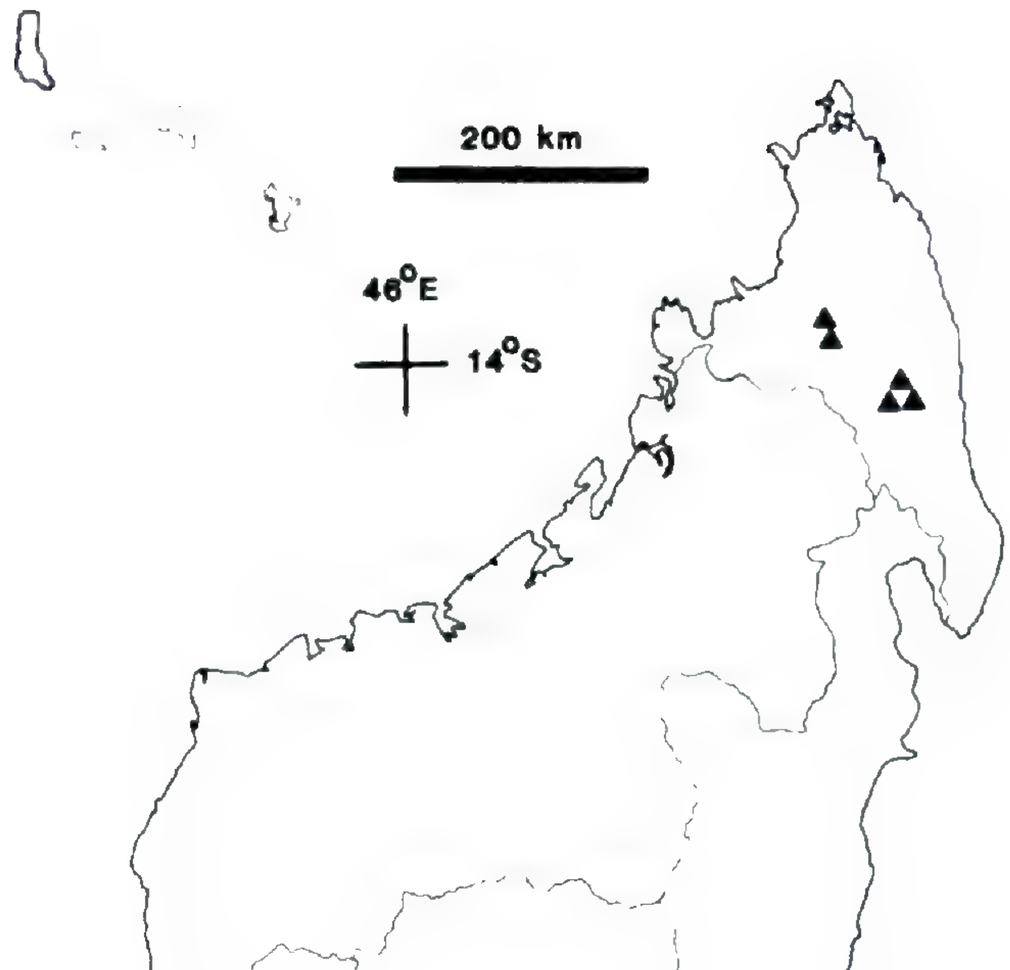


FIGURE 26. Distribution map of some *Ephippiandra* species in Madagascar.

5. Ephippiandra myrtoidea Decne., Ann. Sci. Nat. (Paris), Ser. 4, 9: 278, pl. 7. 1858; A.DC., Prodr. 16(2): 662. 1868; Baill., Hist. Pl. ed. 1, 1: 304. 1869; Perk., Engl. Bot. Jahrb. 25(4–5): 551, t. 5:1–5. 1898; Perk. & Gilg, Pflanzenr. 4, 101: 51, fig. 9. 1901; Perk., Pflanzenr. 4, 101 (Nachtr.): 15. 1911; Perk., Gatt. Monim. 32, fig. 19. 1925; Cavaco in Humbert, Fl. Madagascar 80: 6, fig. I:7–9. 1959. *Mollinedia myrtoidea* (Decne.) Drake in Grandidier, Hist. Phys. Madagascar 1(1): 21. 1902. TYPE: Madagascar. Tananarive: vicinity of Tananarive (fl), *Goudot s.n. in 1840* (holotype, P).

Monoecious treelet 3–4 m tall, densely branching, the new growth sparsely appressed pilose, the mature leafy stems 1.5–2 mm diam., shortly velutinous-tomentose, the hairs pale yellowish brown. Leaves opposite, shortly petiolate; petioles 1–5 mm by 1 mm, velutinous-tomentose; lamina chartaceous to subcoriaceous, ovate to elliptic, 12–30 mm by 8–22 mm, the apex acute to abruptly short acuminate, the tip thickened, the base cuneate to obtuse or rounded, adaxially with a few appressed hairs when young, abaxially with hairs along the costa and margin, the secondary veins 3–6 pairs, making a 65–85° angle with the costa, the venation obscure adaxially, visible to 2° abaxially, the margin entire, pilose, slightly revolute. Inflorescence axillary or terminal, a 3–5-flowered dichasium with a single terminal gynoecious flower subtended by 2–4 androecious flowers, or the flowers axillary, solitary

or in cymes of 2–3, the peduncle 3–4 mm by 1 mm, pubescent, basally bracteolate. Androecious flower in bud globose, 2–4 mm diam., with scattered hairs, the apex apiculate with 1–2 pairs of small, obtuse tepals to 1 mm wide, the pedicel 2.5–20 mm by 0.6 mm, bracteolate; at anthesis deeply 4-fid, 6–8 mm diam., the lobes spreading flat, each usually terminated by a small, obtuse tepal externally; stamens 10–13, 2–3 per lobe, sessile, obtuse, 1 mm long by 1.5–2.5 mm wide, the loculi connivent or usually confluent apically into a single crescentiform loculus, the filament broad, short or sessile, the inner receptacle surface glabrous. Gynoecious flower on a pedicel 6–25 mm by 0.8 mm; at anthesis the receptacle discoid, flat or ± concave, 6–8 mm diam. by 1 mm thick, the surface crowded with 25–30 sessile, 4–6-sided columnar carpels 0.8–1 mm long by 0.7–0.9 mm wide, interspersed with short, simple hairs. Mature fruiting receptacle terminal, the torus swollen, convex, 15–30 mm diam., red when fresh, drying black, the surface sparsely pubescent, bearing (1–)3–14 carpels, the pedicel and peduncle 25–50 mm by 1.5–2.5 mm; carpels ovoid to ellipsoid, 8–9 mm by 5–6 mm, the basal ⅓–½ surrounded by a raised cupule, the mesocarp black when ripe, drying blackish, thin, fleshy, the endocarp thin, brown, the surface finely scrobiculate.

Distribution. Endemic to Madagascar (Fig. 26).

Habitat. The species appears to be restricted to the *Tambourissa/Weinmannia* montane sclerophyllous forest and high altitude ericoid zones of eastern and central Madagascar, from ca. 1,300 to 2,000 m.

MADAGASCAR. FIANARANTSOA: high valley of the Rienana (Basin of the Matitanana River), forest, 1,000–1,400 m, 18–22 Nov. 1924 (fl), *Humbert 3447* (K). PROVINCE UNCERTAIN: Manijarivolo-Andrianony, 1,650 m, 30 Oct. 1970 (fl), *Anon. sub Herb. ORSTOM 3366* (MAD); Central Madagascar (fl), *Baron 1263* (K); (fr), *Baron 1355* (K); Andrangaloatra (fr), *Parker s.n. in 1881* (K); Andohakelo Massif (R.N. 11), 1,800–1,850 m, Jan. 1974 (fl, fr), *Morat 4430* (P); *Morat 4434* (P); *Morat 4480* (P). WITHOUT PRECISE LOCALITY: (fl), *Anon. sub Herb. Alaotra 300* (MAD).

The species is virtually indistinguishable from *Ephippiandra microphylla* except for its androecious flowers which have fewer stamens and lack tepals on the inner apical portion of the receptacle lobes. Pedicel length and inflorescence type intergrade, and further collections and field studies are necessary to ascertain whether the taxa are distinct or merely represent variations of a single, polymorphic species.

6. **Ephippiandra microphylla** (Perk.) Cavaco, Kew Bull. 12: 228. 1957; Cavaco in Humbert, Fl. Madagascar 80: 7, fig. III:6–9. 1959. *Tambourissa microphylla* Perk., Pflanzenr. 4, 101 (Nachtr.): 41. 1911. TYPE: Madagascar. Province uncertain: Ambohimitombo forest (Tanala), 1,350–1,440 m, 22 Dec. 1894 (fr), *Forsyth-Major 326* (holotype, K).

Monoecious treelet or small tree 2–3 m tall, the new growth sparsely pilose to yellowish velutinous-tomentose, the mature leafy stems tomentose or glabrate, 2–3 mm diam. Leaves opposite to subopposite, petiolate; petioles pilose to tomentose, 2–5 mm by 1.2–2 mm; lamina chartaceous, ovate, elliptic or oblong, 20–50 mm by 10–25 mm, the apex acute to abruptly acuminate, the base cuneate to broadly cuneate or obtuse, the secondary veins 4–6 pairs, making a 60–75° angle with the costa, the venation scarcely visible to 2° adaxially, visible to 3° abaxially, the surfaces glabrous, the margin slightly revolute, entire or frequently bearing a pair of small, acute glandular teeth in the apical portion. Inflorescence axillary or terminal, the flowers solitary. Androecious flowers axillary, in bud globose to obovoid, 3–4 mm diam., subglabrous, the apex bearing 4 obtuse tepals, the pedicel 12–27 mm by 0.5 mm, basally bracteolate, subglabrous; at anthesis deeply 4-fid, ca. 10 mm diam., the lobes spreading flat, each bearing a broad, truncate tepal ca. 2 mm wide internally near the apex; staens 16–18, broadly deltoid to ovoid-obtuse, 1–2 mm long by 1.5–2 mm wide, the filament very short or sessile, the loculi confluent apically into a single crescentiform loculus, the connective thick, not prolonged, the internal receptacle surface glabrous. Gynoecious flower subglabrous externally, on a pedicel 20–25 mm by 0.8 mm; at anthesis discoid, flat to slightly concave, 5–6 mm diam., the surface bearing ca. 38 densely crowded, free sessile, 4–6-sided, columnar carpels 0.5 mm diam., interspersed with short, simple hairs. Mature fruiting receptacle enlarged, the torus 15–35 mm diam., bearing 15–25 carpels; carpels ovoid to ellipsoid, 7–8 mm by 4–5 mm, immersed basally in cupules for ca. ½ their length, the mesocarp thin, fleshy, the endocarp thin, brown.

Distribution. Endemic to Madagascar (Fig. 26).

Habitat. The species is known primarily from south central Madagascar where it occurs in the montane *Tambourissa/Weinmannia* wet forest zone from ca. 900 to 1,500 m, but also extends up into the sclerophyllous forest zone from ca. 1,300 to 2,000 m.

MADAGASCAR. TULEAR: Mt. Itrafanaomby (Ankazondrano) and its SW contreforts (high Mandrare basin), rain forest and ericoid scrub on gneissic crests, 1,600–1,963 m, end Dec. 1933 (fl), *Humbert 13518* (MO).

The species is most closely allied to *Ephippiandra myrtoidea,* from which it differs by its androecious flowers, which have more numerous stamens (16–18), and a single broad, truncate tepal on the inner extremity of each receptacle lobe.

EXCLUDED SPECIES

Ephippiandra capuronii Cavaco, Bull. Soc. Bot. France 104: 610. 1957 (= *Tambourissa beanjadensis* Lorence, see discussion under this species).

Tambourissa Sonn., Voy. Ind. Orient. ed. 1, 3: 267, tab. 134. 1782; ed. 2, 4: 405, tab. 134. 1806; Gmel., Syst. Nat. 2(1): 16. 1791, '*Tamburissa*' (sphalm.); A.DC., Prodr. 16(2): 658. 1868; Baill., Hist. Pl. ed. 1, 1: 341. 1869; ed. 2, 1: 332. 1871; Baker, Fl. Mauritius 287. 1877; Benth. & Hook., Gen. Pl. 139. 1883; Pax, Pflanzenfam. 3(2): 101. 1899; Cordem., Fl. Réunion 300. 1895; Perk. & Gilg, Pflanzenr. 4, 101: 66. 1901; Drake in Grandidier, Hist. Phys. Madagascar 1(1): 21. 1902; Perk., Pflanzenr. 4, 101 (Nachtr.): 39. 1911; Perk., Gatt. Monim. 44. 1925; Cavaco, Bull. Soc. Bot. France 104: 284. 1957; Cavaco in Humbert, Fl. Madagascar 80: 18. 1959; Hutch., Gen. Fl. Pl. 1: 118. 1964. TYPE: *T. quadrifida* Sonn.

Tamboure cissa Flacourt, Hist. Madagascar 133, pl. 69. 1661 (pre-Linnaean polynomial).

Mithridatea Comm. ex Schreb., Gen. Pl. 2: 783. 1791; Willd., Sp. Pl. 1(1): 27. 1797; Spreng., Syst. 5(3): 866. 1826, nom. nov. for *Tambourissa* Sonn.

Ambora Juss., Gen. Pl. 401. 1789; Juss., Ann. Mus. Hist. Nat. (Paris) 14: 130. 1809; Poir., Encycl. 7: 565. 1806; Tabl. Encycl. 784. 1806; Steud., Nom. Bot. 37. 1821; Endl., Gen. Pl. 4(2): 56. 1842; Tul., Ann. Sci. Nat. (Paris) 4(3): 29. 1855; Tul., Monogr. Monim. 295. 1855, nom. nov. for *Tambourissa* Sonn.

Schrameckia Danguy, Bull. Mus. Hist. Nat. (Paris) 28: 249. 1922; Perk., Gatt. Monim. 45. 1925; Metay, Arch. Bot. Bull. Mens. 3(11): 177. 1929; Cavaco, Bull. Soc. Bot. France 105: 39. 1958. TYPE: *S. madagascariensis* Danguy (= *Tambourissa floricostata* Cavaco).

Phanerogonocarpus Cavaco, Bull. Soc. Bot. France 104: 612, figs. 1–4. 1957; Cavaco in Humbert, Fl. Madagascar 80: 2, fig. I:1–6. 1957, synon. nov. TYPE: *P. capuronii* Cavaco (= *Tambourissa longicarpa* Lorence).

Small to moderate sized monoecious or dioecious trees, treelets or shrubs, ± aromatic. Leaves simple, usually opposite and decussate, rarely clustered into pseudoverticels, or ternate to alternate, glabrous or pubescent with simple, rarely fasciculate, unicellular trichomes, the margin entire to serrate-dentate with glandular teeth, the venation festooned brochidodromous, the juvenile and sucker leaves usually heterophyllous, apically serrate-dentate. Inflorescence terminal, axillary, ramiflorous or cauliflorous, sometimes leafy, the axes bracteolate, the flowers solitary, fasciculate or disposed in dichasia, pleiochasia or thyrses; flower in bud fleshy, globose, globose-depressed, cylindrical to obovoid, urceolate or napiform (the gynoecious bud usually flattened or depressed apically), apiculate, the apex with several pairs of minute decussate tepals extending into the orifice; male receptacle at anthesis usually splitting into (3–)4–6(–7) ± regular, valvate segments, these remaining partially closed or usually spreading flat and ± reflexing; stamens eglandular, few to very numerous, multiseriate, situated on the glabrous or rarely hairy internal receptacle surface, the anthers tetrasporangiate, bilocular, the 2 loculi free and lateral, connivent, or confluent apically or rarely basally, longitudinally dehiscent, extrorse, sessile or with a distinct filament, the connective sometimes prolonged apically; pollen inaperturate, spheroid to ovoid, the sexine striato-reticulate to rugulate, granulate or granular-tectate; female receptacle at anthesis cylindrical, napiform, cupuliform or rarely discoid, the orifice generally 4(–10)-lobed or entire, the lobes reflexing or not; carpels numerous, immersed in and fused with the receptacle wall, the styles free and protruding, setose or conical to columnar, the internal receptacle surface frequently bearing simple hairs, in some species producing a copious mucilaginous exudate, the ovary unilocular, the ovule solitary, pendulous, anatropous to amphitropous. Fruiting receptacle cupuliform, subglobose, urceolate or cylindrical, corky brown externally, the fruiting carpels (drupes) enclosed within the accrescent receptacle wall which splits open irregularly

at maturity; carpels ovoid-compressed, surrounded by a fleshy, oily red-orange mesocarp, the endocarp horny, whitish to black, the surface smooth or variously sculptured, the embryo straight, the cotyledons flat, oval to elliptic. Gametic chromosome number: $n = 19$.

Distribution. *Tambourissa* is a genus of about 43 species restricted to the southwest Indian Ocean islands of Madagascar (26 spp.), the Comores (5 spp.), the Mascarene Islands of Mauritius (10 spp.), and Réunion (2 spp.). The species display a high degree of endemism, each being restricted to a given island and frequently to a specific habitat within the island.

Habitat. Species of *Tambourissa* are occasional to locally common components of evergreen moist, wet, and cloud forest formations, often conspicuous because of their peculiar flowering and fruiting receptacles.

TAXONOMIC HISTORY OF *TAMBOURISSA*

The name *Tambourissa,* adopted from the pre-Linnaean polynomial "Tamboure cissa" (presumably derived from "tamboul," a Malagasy term for testicles) employed by Flacourt (1661), was first validly published by Sonnerat in 1782. Sonnerat based his genus *Tambourissa* on a single species, *T. quadrifida,* which he undoubtedly described and illustrated while in Mauritius (Ly-Tio-Fane, 1976). A genus characterized by peculiar, often large, cupuliform or urceolate to cylindrical fruiting receptacles containing numerous immersed carpels, *Tambourissa* goes by the colorful local appellations of "Bois tambour" (drumwood) or "Pot de chambre jacot" (monkey's chamber pot) in Mauritius. In neighboring Réunion it is called "Bois de bombarde" (bombardment wood) because the ripe fruiting receptacle splits open irregularly to reveal an array of numerous, red-orange carpels set against the pale orange receptacular pulp (Fig. 17B). In Anjouan and Grand Comore (Comore islands) *Tambourissa* is known as "M'bweza," meaning to calm or sooth the pain, because its leaves are used medicinally in tea. Many species in Madagascar and Mayotte (Comores) go by the name of "Ambora." The species in Mohéli is called "Diarou."

Sonnerat felt the genus occupied a position somewhere between *Ficus* and *Dorstenia* because of its closed, fig-like buds and gynoecious floral receptacle with an inferior, syncarpous gynoecium. In 1789, the genus was redescribed by A. L. de Jussieu as *Ambora* from the Malagasy vernacular name, and again as *Mithridatea* by Commerson, Sonnerat's mentor, in Schreber (1791). It is unclear why these authors redescribed *Tambourissa* under other names, because both genera were based on Sonnerat's original species, *T. quadrifida.* It was not until 1855 that Tulasne correctly placed the genus in Monimiaceae, publishing 11 new species of *Ambora* (1855a) for his monograph of the family (1855b).

In 1868, Alphonse de Candolle transferred all of Tulasne's species to *Tambourissa,* describing no new taxa but providing one new name. Baker (1877) described two new species of *Tambourissa* from Mauritius in his treatment of the family for "Flora of Mauritius and the Seychelles" and later described three more from Madagascar. At the turn of the century, Perkins and Gilg (1901) monographed the entire family for Engler's "Pflanzenreich," providing a synoptic treatment for *Tambourissa* and describing one new species. In her revision of the family ten years later, again for the "Pflanzenreich," Perkins (1911) published four additional species from the Comores and Madagascar. During this same period, Drake del Castillo (1902) published two new species, and Danguy (1922) published another (as *Schrameckia* because of its few, large stamens), all from Madagascar. After a hiatus of some 35 years, Cavaco revised the Malagasy Monimiaceae for "Flore de Madagascar et des Comores" (1959), publishing nine new Malagasy species of *Tambourissa* (1957a, 1957c, 1957d, 1957e, 1958c). Most recently, Lorence (1982) published seven new species and one subspecies of *Tambourissa* from the Malagasy region. *Phanerogonocarpus,* described by Cavaco (1957c), was named for its narrowly winged, tubular gynoecious flowers and fruits and based on two Madagascan species. In the present revision of *Tambourissa,* three new names are proposed, and at the same time nine other taxa are reduced to synonymy.

GENERIC DELIMITATIONS AND SYSTEMATIC POSITION OF *TAMBOURISSA*

The genus *Phanerogonocarpus* was described by Cavaco (1957b) on the basis of its winged or ribbed, narrowly obconical to cylindrical gynoecious flowering and fruiting receptacles (Fig. 17A), which he compared to the ribbed flowers of *Schrameckia.* Cavaco (1959) later undermined this character when he reduced *Schrameckia* to synonymy under *Tambourissa.* Furthermore, two species of *Tambourissa, T. perrieri,* and *T. quad-*

rifida, both possess ellipsoid to obovoid gynoecious floral receptacles approaching those of *Phanerogonocarpus,* although not as narrow. Carpels of both genera are identically immersed in and united with the receptacle wall (Figs. 13E, 16A–D). Furthermore, styles of *Phanerogonocarpus* are conical with an acute apex, possess an oblique stylar canal, and are interspersed with short simple hairs as in *Tambourissa* (Fig. 16D).

Fruiting receptacles of both genera are externally corky brown and split open irregularly at maturity to reveal the numerous ripe carpels immersed in a pale orange matrix. That the fruit of *Phanerogonocarpus* splits lengthwise leaving the central tube more or less intact is related to its elongated shape; the ellipsoid to obovoid fruits of *Tambourissa quadrifida* behave similarly. Mature fruiting carpels of both genera consist of a bright orange, fleshy mesocarp enclosing the dark brown, finely sculptured endocarp. Supposed differences between the genera in gynoecious floral and fruit morphology are clearly those of degree and fail to support generic segregation.

In his original description of *Phanerogonocarpus,* Cavaco (1957c) noted the resemblance of its androecious flowers and stamens to those of *Tambourissa,* except for the presence of tepals ("staminodes") on the inner tips of the receptacle lobes in the former. This feature is, however, shared with a number of *Tambourissa* species such as *T. comorensis, T. floricostata,* and *T. paradoxa* to name a few. Cavaco correctly interpreted the staminal morphology of *Phanerogonocarpus* as falling within the range of variability displayed by *Tambourissa,* however.

Pollen of *Phanerogonocarpus capuronii* (= *Tambourissa longicarpa*) is subspheroid to ovoid with a striato-rugulate sexine composed of short, compactly spaced finger-like elements. That of *P. perrieri* (= *T. alaticarpa*) is spheroid to suboid with a rugulate sexine composed of more continuous elements than in *P. capuronii.* Sexinous patterns of both species are strikingly similar to those found in many *Tambourissa* species, e.g., *T. comorensis, T. cordifolia, T. ficus, T. floricostata,* and *T. quadrifida.* A survey of pollen from a range of *Tambourissa* species shows the genus to have sexinous sculpturing ranging from striato-reticulate or rugulate to granular-tectate, thus readily accommodating the patterns displayed by *Phanerogonocarpus* (Lorence et al., 1984).

Regarding inflorescence structure, the sexually mixed pleiochasium terminated by one or two gynoecious flowers in *Phanerogonocarpus* (Fig. 17A) also occurs in a number of *Tambourissa* species, e.g., *T. hildebrandtii* and *T. perrieri.* Finally, leaf architecture of the two genera overlaps. Adult leaves of a number of *Tambourissa* species, e.g., *T. thouvenotii* and *T. trichophylla,* as well as juvenile and sucker leaves of many species are dentate, as are adult leaves of *Phanerogonocarpus.* I can find no obvious basis for maintaining *Phanerogonocarpus* as a distinct genus and therefore propose that it be reduced to synonymy under *Tambourissa.*

Tambourissa has attained the highest level of floral morphological specialization of all the Malagasy Monimiaceae in the subfamily Mollinedioideae. Most species are characterized by a strong androecious/gynoecious floral dimorphism, have flowers of both sexes closed in bud, have highly reduced tepals, show a range of staminal specialization via reduction and, most significantly, the gynoecious flowers have their carpels immersed in and fused with the massively developed ovary wall, with the fruiting carpels likewise enclosed in the accrescent receptacle which splits open irregularly at maturity.

INTRAGENERIC RELATIONSHIPS

Tambourissa, with about 43 species, is the largest genus of Monimiaceae in the Old World. Its members often display extensive interspecific variation in floral morphology (color, size, shape, and number of parts), pubescence, leaf morphology, and other characters. Even species which are obviously closely related with respect to features such as foliar and gynoecious floral morphology may differ radically and inexplicably in other features such as androecious floral or staminal morphology. This happens frequently enough to render the establishment of meaningful subgeneric categories such as subgenera or sections impossible at present. I have, therefore, chosen to place the species into informal groups of morphologically similar taxa to facilitate their comparison, but no phylogenetic implications are intended by this sequence. Nine species groups are listed below, each followed by a discussion (refer also to Tables 5–7):

1. Group A. ..... *Tambourissa thouvenotii, T. trichophylla, T. uapacifolia*
   Group B. ..... *Tambourissa decaryana, T. hildebrandtii, T. hum-*

bertii, T. nitida, T. nosybensis

Group C. ..... *Tambourissa floricostata, T. parvifolia*

2. Group A. ..... *Tambourissa beanjadensis, T. comorensis, T. crassa, T. elliptica, T. leptophylla, T. madagascariensis*

Group B. ..... *Tambourissa kirkii, T. paradoxa*

3. ..... *Tambourissa capuronii, T. moheliensis*

4. ..... *Tambourissa gracilis, T. purpurea, T. religiosa*

5. ..... *Tambourissa amplifolia, T. cocottensis, T. cordifolia, T. pedicellata, T. tau, T. tetragona*

6. ..... *Tambourissa bathiei, T. sieberi*

7. ..... *Tambourissa perrieri, T. quadrifida*

8. ..... *Tambourissa alaticarpa, T. longicarpa*

9. ..... *Tambourissa castri-delphinii, T. ficus, T. peltata*

Group 1. This is a group of Madagascan species with canescent to velutinous or tomentose stems, leaves, and inflorescences (Table 5). The inflorescence is usually a ramiflorous or axillary (rarely cauliflorous) pleiochasium, often sexually mixed and frequently terminated by a gynoecious flower, or the flowers may be solitary. Long acute, subulate or deltoid bracteoles subtend the pedicels and floral axis. The androecious flower splits open flat into 4(–5) segments, bears scattered hairs internally in many species, and has fairly numerous stamens, frequently with prolonged connectives. The urceolate, napiform or subglobose gynoecious flower opens by a small four-lobed, X-shaped orifice in most, and the densely velutinous internal surface is lined with many shortly conical styles. In most species, an abundance of oil cells occurs in the floral ground tissue of both sexes.

Group 1A. This group is comprised of three species with densely pubescent, usually apically toothed, adult leaves (*Tambourissa thouvenotii, T. trichophylla*) and densely velutinous-tomentose mature stems (Table 5). *Tambourissa uapacifolia* fits here on the basis of its dense pubescence, although its leaves are entire and the inflorescence is apparently unisexual.

Group 1B. Five species with entire leaves and sparsely pubescent to canescent adult leaves and stems comprise this group (Table 5): *Tambourissa decaryana, T. hildebrandtii, T. humbertii, T. nitida,* and *T. nosybensis.* Of these, *T. decaryana, T. humbertii,* and *T. nosybensis* show trends towards cauliflory and unisexual inflorescences.

Group 1C. The last group contains two species differing in having subglabrous mature growth and internally glabrous female flowers (Tables 5, 6). *Tambourissa floricostata* has few, large stamens and floral receptacles with longitudinal lateral ridges; it was formerly placed in *Schrameckia* (Danguy, 1928). In *T. parvifolia,* the leaves are small and sclerophyllous and the stamens slender with distinct filaments lacking prolonged connectives.

Group 2. This diverse group includes species from the Comores, Madagascar, and Réunion, some of which appear to be much more closely related than others (Tables 5, 6). Most have glabrous to sparsely pubescent mature growth and inflorescences. Varying degrees of reduction occur in the inflorescence, which ranges from a sexually mixed or unisexual pleiochasium to a fascicle or solitary flowers. Small deltoid bracteoles subtend the often long, slender floral axis and pedicels. Two subgroups can be distinguished.

Group 2A. This category consists of species with medium-sized to large, 4-fid androecious flowers that open flat and contain numerous long stamens with separate or apically confluent loculi and scarcely or non-prolonged connectives (Tables 6, 7). The gynoecious flowers are globose-depressed, closed in bud, internally ± glabrous with crowded, shortly columnar blunt styles, open by an X-shaped orifice, and produce a copious mucilaginous secretion in the two Réunion species (*Tambourissa crassa, T. elliptica*) and *T. beanjadensis* (Madagascar). In *T. madagascariensis* (Madagascar) and the Comorean species (*T. comorensis, T. leptophylla*) the orifice of the gynoecious receptacle is entire, internally pubescent and remains open during the entire floral development, a condition which is probably highly specialized (P. Endress, pers. comm.). Styles of the two latter species are bluntly columnar and shortly conical, respectively.

Group 2B. This group consists of two Comorean species in which the androecious flowers are

small and globular, splitting only slightly and remaining nearly closed (*Tambourissa kirkii*), or merely opening by a small apical pore lined with scale-like tepals (*T. paradoxa*) (Table 6). In both species stamens are fewer, smaller, and more acute than in Subgroup A and have separate, medial loculi and acute, prolonged connectives. Androecious flowers of *T. moheliensis* correspond well with this group, but because its gynoecious flowers differ markedly from the other members, it will be discussed under Group 3. Gynoecious flowers of *T. kirkii* have an entire, circular orifice like *T. comorensis* and *T. leptophylla,* thus linking it to Group 2A; those of *T. paradoxa* are unknown.

Group 3. Members of this group are characterized by comparatively large, brown napiform gynoecious flowers that are closed and apically depressed in bud, later opening by a four-lobed, X-shaped orifice (Table 6). Unlike Group 2, the floral ground tissue contains numerous dark brown, presumably tanniferous, idioblasts. Androecious flowers of *Tambourissa capuronii* (Madagascar) are large, split open flat into four lobes, and have numerous large stamens with elongated lateral loculi. Those of *T. moheliensis* (Comores) are much smaller than in the former species, only split slightly open at anthesis (as in Group 2B), and differ in having fewer stamens with loculi that unite basally into a U-shape. Its androecious flowers therefore link Group 2B with Group 3.

Group 4. This group is composed of three Madagascan species which are glabrous to subglabrous, ramiflorous shrubs or small trees, mostly with arching branches, and have characteristic terminal dichasia, condensed pleiochasia or solitary flowers (Tables 5, 6). The gynoecious flowers and fruit are terminal, whereas the androecious flowers are either lateral, axillary, or ramiflorous. Floral receptacles are small and globose, monomorphic in both sexes, and open by small apical pores flanked by minute tepals. The comparatively small ripe fruiting receptacles are smooth and dark reddish externally, not pale and corky brown as in most other species. *Tambourissa gracilis* and *T. purpurea* both have similar androecious flowers with short, sessile stamens having apically confluent, crescentiform loculi; gynoecious flowers of the former are unknown. Flowers of *T. religiosa* are somewhat larger with longer, shortly conical styles. Also, its stamens have distinct filaments and separate loculi. Gynoecious flowers of *T. purpurea* produce a mucilaginous plug or "hyperstigma" which occludes the pore; it is not known if this phenomenon occurs in the other two species.

Group 5. This group of subglabrous to glabrous trees, treelets and shrubs includes the bulk of the Mauritian species (Tables 5, 6). *Tambourissa pedicellata* seems to be the least specialized member in view of its monoecy, variability of floral disposition and inflorescence structure, and particularly its monomorphic androecious and gynoecious flowers with shallowly subglobose to cupuliform receptacles, relatively few parts, shortly conical styles, and stamens with separate loculi and distinct filaments.

Other members of the group (*Tambourissa amplifolia, T. cocottensis, T. cordifolia, T. tau,* and *T. tetragona*) display variations on this theme with varying degrees of specialization in one or more features. Leaves of most species are moderately small, opposite and decussate, and have distinct petioles. Trends of specialization are towards macrophylly (*T. amplifolia, T. tau*), clustering of the leaves into pseudoverticils of two to four pairs (*T. tau*), winged stems (*T. tetragona*), and reduction in petiole length (*T. cordifolia, T. tau*). Modifications of the inflorescence tend towards reduction from pleiochasia to dichasia, and finally to fascicles and monochasia, towards a shortening of the pedicels and floral axis, and from ramiflory to (often basal) cauliflory.

Other apparent trends are towards greater floral dimorphism, towards larger flowers with more numerous parts (*T. cordifolia*), and towards staminal structural modifications such as fusion of the loculi apically (*T. amplifolia*), basally (*T. cordifolia*), or their extreme separation on lateral arms (*T. tau*). Gynoecious flowers display a greater deepening and closure (*T. cocottensis, T. tetragona*) or opening (*T. peltata*), modifications of the styles via elongation (*T. tau*) or shortening (*T. peltata*), and elaborate development of the receptacular lobes with bright coloration to enhance their attractive potential for pollinators (*T. cordifolia, T. peltata*). The latter two species are further specialized in being dioecious. Gynoecious flowers of *T. ficus* correspond to this group in spite of their gigantism. Because of the ternate leaves and androecious floral morphology, however, I have included *T. ficus* under Group 9.

Group 6. This group consists of two species of large, monoecious trees, i.e., *Tambourissa sieberi* (Mauritius) and *T. bathiei* (Madagascar).

Both have relatively small leaves, moderately to densely pubescent new growth and densely yellowish velutinous, cauliflorous inflorescences which are generally unisexual pleiochasia or thyrses (Tables 5, 6). The globose female receptacle opens by a small pore in *T. sieberi* (mature gynoecious flowers unknown in *T. bathiei*), and is lined with numerous long, narrowly conical, generally coalescent styles. Androecious flowers of both species are large and 4–5-fid with lobes that spread open flat and have numerous large stamens.

Group 7. Apparently related to Group 6, this category also contains two species not closely allied to other members of the genus: *Tambourissa quadrifida* (Mauritius) and *T. perrieri* (Madagascar). Both are glabrous cauliflorous trees with relatively small, opposite leaves, grow in relatively drier habitats, and produce numerous unisexual or sexually mixed pleiochasia or thyrses along most of the trunk (Tables 5, 6). Androecious flowers of both species split deeply into four flat or strongly recurved segments and bear hundreds of short stamens. The ellipsoid to obovoid or obpyriform gynoecious flowers open by a small, three- to four-lobed apical pore, are internally velutinous and contain hundreds of very short, basally ventricose styles. The mature fruiting receptacles of both are elongated with a small orifice, resembling those of Group 8.

Group 8. This isolated pair of Madagascan species, *Tambourissa alaticarpa* and *T. longicarpa,* formerly comprised the genus *Phanerogonocarpus.* Both are pubescent, monoecious, cauli- to ramiflorous treelets of the eastern wet forest zone with large, dentate leaves (Tables 5, 6). The pubescent, sexually mixed (rarely unisexual) inflorescence consists of one or two (rarely three) terminal gynoecious flowers with lateral clusters of relatively small androecious flowers grouped along the floral axis, a feature shared with certain members of Groups 1 and 7. The stamens have distinct filaments, free loculi, and the connective may or may not be prolonged. Most distinctive of Group 8 are the slender, obovoid to cylindrical, narrowly ribbed or winged gynoecious flowering and fruiting receptacles with a small orifice. Gynoecious receptacles of *T. floricostata* (Group 1C) are also ribbed, however, and those of Group 7 are ellipsoid to obovoid, although not as narrow, with comparably small orifices. The conical to ventricose styles are interspersed with dense short hairs in both species, and a mucilaginous exudate is apparently produced in *T. longicarpa.*

Group 9. Characterized by ternate to subalternate adult leaves with prominent, highly organized and finely reticulate venation, this group consists of three species (Tables 5, 6), i.e., *Tambourissa castri-delphinii* (Madagascar), *T. ficus,* and *T. peltata* (both Mauritius). Flowers are produced either at the base of the trunk (*T. ficus*), or on the upper trunk and older branches (*T. peltata* and *T. castri-delphinii*). The highly reduced inflorescence ranges from a short, condensed pleiochasium or fascicle in the latter, to a two-flowered fascicle or monochasium in the other two species. The group also displays a trend towards dioecy.

Androecious flowers of *Tambourissa ficus* are the largest in the entire genus, with five to seven incurved or spreading lobes bearing from 900 to 1,800 ligulate stamens with separate, lateral to unifacial loculi and a thick, prolonged connective. Androecious flowers of *T. peltata* and *T. castri-delphinii* are considerably smaller, deeply split into four or five recurved lobes, and bear numerous thin, broadly deltoid subsessile stamens with connivent or confluent lateral loculi.

Gynoecious flowers of *Tambourissa peltata* are highly specialized, flat and discoid with four to seven elaborate, spreading verrucose sterile lobes and numerous crowded, highly reduced, flat columnar styles which produce a copious mucilaginous exudate. Those of *T. castri-delphinii* have an X-shaped orifice and conical styles, similar to some species in Group 5. In *T. ficus* the gynoecious flowers are huge and urceolate, splitting into numerous straight or inflexed lobes with a broad orifice, and contain ca. 1,000–2,000 setose styles. Apart from their great size, gynoecious flowers of *T. ficus* are morphologically similar to those of species belonging to Group 5 and link the two groups.

In the following key I have attempted to utilize vegetative characters as far as possible. Although certain species with outstanding vegetative characters are identifiable even from sterile specimens (e.g., *Tambourissa tetragona* is the only species with winged stems), for the majority, complete collections consisting of leafy stems, androecious and gynoecious flowers, and fruits are essential for reliable identification. Unfortunately, a large number of species, especially those from Madagascar and the Comores, are known only from androecious or gynoecious

flowers or fruits, and this has imposed certain limitations on the construction of this key. Although I was unable to examine all the Madagascan material cited by Cavaco (1959), I have seen additional material not cited by him. All collections in the Exsiccata and virtually all those used to plot the distribution maps have been seen by me. The last five species in the taxonomic treatment (nos. 39–44) are imperfectly known and consequently have not been included in the key. See key cited on following pages.

1. **Tambourissa trichophylla** Baker, J. Linn Soc., Bot. 20: 240. 1884; Perk. & Gilg, Pflanzenr. 4, 101: 68. 1901; Drake in Grandidier, Hist. Phys. Madagascar 1(1): 24. 1902; Perk., Pflanzenr. 4, 101 (Nachtr.): 41. 1911; Cavaco in Humbert, Fl. Madagascar 80: 24, fig. VII:8–9. 1959. TYPE: Madagascar. ("Central Madagascar," probably Tananarive or Fianarantsoa): without precise locality, 1882 (fl), *Baron 1953* (lectotype, K, here designated).

Monoecious treelet or tree attaining 15 m tall and 15–20 cm D.B.H., the new growth densely pilose-tomentose, the hairs simple, pale yellowish to grayish, the mature leafy stems 2–4 mm diam., tomentose, the hairs ± matted. Leaves opposite to subopposite, petiolate; petioles tomentose, 4–10 mm by 1.5–2 mm; lamina chartaceous to subcoriaceous, oblong, narrowly oblong, narrowly obovate, lanceolate or rarely elliptic, (50–)70–195 mm by 20–52 mm, the apex shortly acuminate, shortly acute or rarely obtuse, the base obtuse to rounded, rarely acute, abaxially tomentose-hirsute, especially along costa and secondary veins, the trichomes curved, adaxially pilose when young, glabrescent, the secondary veins 3–5 pairs, making a 50–60° angle with the costa, the arches low and broad, the venation disorganized, obscure adaxially and visible to 2°, prominent abaxially and visible to 3°, the margin slightly thickened and revolute, ciliate, entire or usually serrate-dentate in the apical ⅓–¼ of the lamina with 1–2 pairs of short, broadly deltoid teeth. Inflorescence ramiflorous on leafless nodes or axillary, a usually unisexual, sometimes leafy pleiochasium of 3–7 flowers, or the flowers solitary, the floral axis fulvous to grayish, velutinous-tomentose, 14–55 mm by 1.5–2 mm, subtended by several deltoid-naviculate bracteoles 1–2 mm long, the pedicels 3–5 mm by 1.5 mm, each subtended by 1(–2) subulate velutinous bracteoles 4–5 mm long. Androecious flower in bud globose, 5–7 mm diam., hirsute, apiculate with several pairs of minute hirsute tepals; androecious flower at anthesis unknown (presumably deeply 4-fid with spreading lobes as in *T. thouvenotii*); stamens in bud ca. 100, ovoid-deltoid, 1.5–2 mm long by 0.8–1 mm wide, the loculi lateral, separate, occupying ca. ¾ total length of stamen, the filament short or sessile, the connective thick, slightly prolonged apically, the internal receptacle surface with clusters of hairs between the stamens. Gynoecious flower in bud solitary or occasionally in pleiochasia, 7–8 mm diam. by 5–6 mm long, subglobose-depressed, hirsute, apiculate with 4 minute deltoid tepals; at anthesis shallowly 4(–5)-fid, the lobes ± incurved, the small X-shaped orifice 2–3 mm diam., the styles ca. 100, conical, 0.6–0.8 mm long by 0.3–0.4 mm wide basally, ± ventricose, acuminate, the internal receptacle surface velutinous between the styles. Fruiting receptacle solitary on the smaller branches, shallowly cupuliform, 30–48 mm diam. by 30 mm long, the walls 13–15 mm thick, both surfaces pale corky brown, the orifice subentire, comprising ca. ½ total diam. of the fruit, the scattered styles conical, 0.3–0.5 mm long and wide basally, the internal receptacle surface hirsutulous; pedicel and peduncle stout, 6–8 mm long by 7–12 mm diam., hirsutulous. Submature carpels 6–8 mm long, 4–5 mm wide, 3–4 mm thick, ovoid-compressed, the endocarp brown.

Distribution. Endemic to Madagascar (Fig. 27).

Habitat. The species is locally common and fairly widespread in the *Tambourissa/Weinmannia* wet forest zone in the eastern and central regions ranging from 800 to 1,500 m.

MADAGASCAR. TAMATAVE: Ankaraoka, ca. 1,500 m, 28 Dec. 1944 (fl, fr), *Anon. sub Herb. Alaotra 3073* (MAD); National Route no. 2 at 69 km E of Tananarive, Mandraka forest reserve, 1,400 m, 28 Oct. 1978 (fl), *Lorence 1879* (MAD, MAU, MO); 30 Oct. 1978 (fl), *Lorence 2034* (MAD, MO); (fl), *Lorence 2035* (MAD, MO); La Mandraka, Sept. 1963 (st), *Morat 7* (MAD); National Route no. 2 at ca. 20 km W of Perinet, 950 m, 29 Oct. 1978 (st), *Lorence 2000* (MAD, MO). TANANARIVE: Andringitra Massif, Ambodigraiss Forest near Antsirabe (sic), 1,200 m, 12 Jan. 1945 (fr), *Anon. sub Herb. Alaotra 2242* (MAD). PROVINCE UNCERTAIN: head of Ankafinka Valley, 16 Nov. 1965 (fr), *Rakotozafy 266* (MAD). WITHOUT PRECISE LOCALITY: Central Madagascar, 1882 (fl), *Baron 1975a*

KEY TO THE SPECIES OF *TAMBOURISSA*

[N.B.: for Madagascan material also refer to descriptions of last four species (nos. 39–43), not included in this key].

1a. **Mature leaves, petioles, and stems conspicuously pubescent (canescent, villous, or velutinous-tomentose).**
- 2a. Gynoecious floral and fruiting receptacles narrowly obovoid-cylindrical, tubular, bearing 4–6 longitudinal ridges or narrow wings; Madagascar.
  - 3a. Leaves serrate-dentate with 9–10 pairs of narrow, acute teeth in apical ⅔ of lamina; staminal connective not prolonged beyond anther; gynoecious flower at most puberulent, glabrescent ..... 34. *T. alaticarpa*
  - 3b. Leaves strongly dentate with (1–)2–3 pairs of broad, deltoid teeth in apical ⅓ of lamina; staminal connective prolonged beyond anther; gynoecious flower densely pubescent ..... 35. *T. longicarpa*
- 2b. Gynoecious floral and fruiting receptacles subglobose to cupuliform, at most ellipsoid to obovoid or pyriform, unwinged (if bearing 2 or many low, rounded ribs, then receptacle globose or discoid); Madagascar, Mascarenes, Comores.
  - 4a. Inflorescence a robust, cauliflorous, velutinous thyrse with 16–90 flowers; floral axis stout, 50–110 mm long; mature buds globose, 12–14 mm diam.; large tree, Mauritius ..... 30. *T. sieberi*
  - 4b. Inflorescence and buds much smaller and sparser, a cauliflorous or ramiflorous pleiochasium; large or small trees; Madagascar.
    - 5a. Mature leaves abaxially velutinous-tomentose, at least on margins, costa and major veins; leafy stems and petioles velutinous-tomentose.
      - 6a. Adult leaves entire, the apex obtuse to retuse; loculi of stamens bearing scattered hairs externally, the connective not prolonged ..... 3. *T. uapacifolia*
      - 6b. Adult leaves with 1–8 pairs of teeth in apical half of lamina, the apex shortly acute to acuminate, rarely obtuse; loculi of stamens glabrous, the connective prolonged.
        - 7a. Lamina elliptic to broadly elliptic, 50–90 mm wide; arches of secondary veins high and narrow; petioles 10–20 mm long; floral pedicels 12–17 mm long; fruit distinctly pedicellate ..... 2. *T. thouvenotii*
        - 7b. Lamina narrowly oblong to oblong or oblanceolate, 20–50 mm wide; arches of secondary veins low, broad; petioles 4–10 mm long; floral pedicels 3–5 mm long; fruit subsessile to sessile ..... 1. *T. trichophylla*
    - 5b. Mature leaves at most puberulent abaxially; stems and petioles canescent to sparsely villous.
      - 8a. Lamina very lustrous adaxially, dull abaxially, the apex long acuminate ..... 4. *T. nitida*
      - 8b. Lamina dull on both surfaces, the apex at most acuminate.
        - 9a. **Apex of lamina very shortly acuminate to obtuse or retuse; gynoecious receptacle subglobose-napiform, not ribbed, the styles 1–1.5 mm long, strongly papillose in both flower and fruit; stamens with a very short, apiculate connective** ..... 5. *T. hildebrandtii*
        - 9b. **Apex of lamina acuminate; gynoecious receptacle discoid, ribbed, the styles 0.4–0.6 mm long, not papillose; stamens with an acute, prolonged connective 0.5 mm long** ..... 6. *T. nosybensis*

1b. **Mature leaves, petioles, and stems glabrous, or at most with rare, scattered hairs.**
- 10a. Adult leaves ternate, dissociate or even subalternate, except rarely opposite in *T. castri-delphinii*.
  - 11a. Flowers in short pleiochasia or fascicles of (3–)4–9 flowers on a common axis, never solitary, the pedicels slender, 0.5–1 mm diam.; Madagascar, E coast, Manakara to Fort Dauphin ..... 36. *T. castri-delphinii*
  - 11b. Flowers solitary or in pairs, never on a common axis, the pedicels stout, 1.5–4.5 mm diam.; Mauritius.

12a. **Buds, pedicels, and new vegetative growth puberulent; inflorescence basally cauliflorous; stamens 900–1,800, 0.5–1 mm wide, the loculi separate, the thick, obtuse connective prolonged for ¼–⅓ total length of stamen; gynoecious flower massive, urceolate, with 6–8 erect to incurved lobes, the styles 1,000–2,000, setose, 1.5–5 mm long** ..... 37. *T. ficus*

12b. **Buds, pedicels, and new vegetative growth glabrous; inflorescence ramiflorous, rarely cauliflorous on top part of trunk; stamens 200–400, 1.5–3 mm wide, the loculi confluent apically or the connective only slightly prolonged; gynoecious flower flat and discoid with 4–7 broad, spreading-reflexed lobes, the styles 400–500, crowded, columnar, flat-topped, coalescent, 0.5 mm long** ..... **38. *T. peltata***

10b. Adult leaves strictly in decussate pairs, opposite or rarely subopposite.

13a. Leafy stems quadrangular, conspicuously winged; Mauritius, summit of Mt. Cocotte ..... 27. *T. tetragona*

13b. Leafy stems terete or subterete, neither quadrangular nor winged.

14a. Leaf base strongly cordate and amplexicaul; dioecious shrubs 50–150 cm high; Mauritius, in *Philippia* heath formation or low scrub ..... 29. *T. cordifolia*

14b. Leaf base acute to weakly cordate, not amplexicaul; larger treelets or trees; forests of Mauritius, Réunion, Madagascar, Comores.

15a. **Leaves pseudoverticillate, clustered in 2–4 pairs separated by long intervals.**

16a. Stamens ± T-shaped with separate loculi; buds and flowers externally corky brown; styles setose, 2–3 mm long; orifice of gynoecious flower with 5–10 irregular incurved deltoid lobes ..... 26. *T. tau*

16b. Stamens clavate with apically confluent loculi; buds and flowers not externally corky; styles shortly conical, 0.6–1 mm long; lobes of female receptacle 4, deltoid, ± erect ..... 25. *T. amplifolia*

15b. Leaves regularly disposed in pairs along stem.

17a. Mature inflorescence externally glabrous (or corky), at most with rare scattered hairs, not conspicuously nor finely pubescent under dissecting microscope.

18a. **Flowers large, solitary, and terminal on branches (rarely terminal on leafy cauliflorous shoots); buds and female receptacles 12–15 mm diam.; androecious flowers splitting into 4–5 lobes, opening to 40–50 mm diam.; dioecious trees or treelets; leaves large, thick, obtuse to retuse, the higher order venation (3° and above) obscure, when dry fragrant and often bright yellow-green; Réunion** ..... 14. *T. crassa*

18b. Flowers in dichasia or pleiochasia, rarely solitary or in fascicles of 2, either ramiflorous, axillary or terminal (if solitary, then buds and flowers much smaller, less than 9 mm diam.); leaves smaller and thinner, when dry not fragrant, dull dark green or brownish, not bright yellow-green; Mauritius, Réunion, Madagascar, Comores.

19a. Floral pedicel and peduncle acutely quadrangular, 5–7 mm long, bearing four rows of decussate ciliate bracteoles; buds and flowers externally corky brown, cauliflorous, solitary or in groups of 2; Mauritius, summit of Mt. Cocotte ..... 28. *T. cocottensis*

19b. Floral pedicel and peduncle terete to subtetragonal, neither quadrangular nor with four rows of bracteoles; Mauritius, Madagascar, Réunion, Comores.

20a. Adult leaves small, coriaceous, 15–45 mm by 9–22 mm, obovate, elliptic or oblong, the apex obtuse to retuse; inflorescence ramiflorous on leafless stems, a lax, glabrous to canescent pleiochasium ca. 25–70 mm long; small monoecious trees; montane forests, central Madagascar ..... 10. *T. parvifolia*

20b. Adult leaves mostly much larger, the inflorescence mostly exceeding 15 mm long; if leaves as small, then inflorescence axillary or terminal on leafy stems, a short, congested dichasium or pleiochasium 10–15 mm long, or the flowers rarely solitary; Madagascar, Mauritius, Réunion, Comores.

21a. Inflorescence and buds externally corky and pale brown; androecious buds 15–19 mm diam.; connectives of stamens acute, prolonged, with several hairs at apex; Madagascar ..... 20. *T. capuronii*

21b. Inflorescence and buds externally smooth, dark brown or blackish, never corky; androecious buds 2–11 mm diam.; connectives of stamens prolonged or lacking, but never bearing hairs; Madagascar, Mauritius, Réunion, Comores.

22a. Inflorescence terminal or axillary, a short, congested dichasium or pleiochasium 10–15 mm long (flowers rarely solitary); Madagascar.

23a. Leaves larger, 70–150 mm by 30–60 mm; lamina coriaceous, the 3–5° veins prominent abaxially, a marginal fimbrial vein present; buds and flowers 7–10 mm diam. by 4–7 mm long; stamens 60–82, with distinct filament and separate loculi ..... 21. *T. religiosa*

23b. Leaves usually much smaller, 40–85 mm by 15–40 mm; lamina subcoriaceous, the 3–4° veins not prominent, a marginal fimbrial vein absent; buds and flowers 3–5.5(–7) mm diam. by 2.5–6(–7) mm long; stamens 20–32, ± sessile, the filament not distinct, the loculi confluent apically into a single crescentiform loculus ..... 22. *T. purpurea*

22b. Inflorescence rami- or cauliflorous, a lax, occasionally leafy, pleiochasium or thyrse greatly exceeding 15 mm long (flowers occasionally solitary, axillary); Mauritius, Réunion, Comores, Madagascar.

24a. Androecious receptacle splitting for less than half its length into 4–5 short, incurved or erect lobes, or opening by a small, subentire apical pore.

25a. Floral pedicels 15–66 mm long, glabrous; androecious receptacle shallowly 4–6-fid, the lobes lacking scale-like tepals internally; stamens with separate loculi; leaf apex shortly acuminate, acute, obtuse or retuse; Mauritius ..... 24. *T. pedicellata*

25b. Floral pedicel 5–13 mm long, with scattered hairs; androecious receptacle with obtuse, scale-like tepals internally on the lobes or flanking the orifice; stamens with confluent loculi; leaf apex acute to long acuminate.

26a. Androecious flowers opening by a small, circular orifice 1–2 mm diam.; stamens ± sessile with apically confluent loculi; leaf apex acuminate; Madagascar ..... 23. *T. gracilis*

26b. Androecious flower splitting into 4 shallow lobes; stamens with loculi confluent basally into a U-shape; leaf apex acute or rounded; Mohéli (Comores) ..... 19. *T. moheliensis*

24b. Androecious receptacle deeply split at anthesis for more than half its length into (3–)4–5 deltoid lobes that ultimately spread open flat or reflex.
27a. Gynoecious receptacle longer than wide, obovoid to pyriform or ellipsoid; cauliflorous species; inflorescence a stout pleiochasium or thyrse 60–180 mm long; floral axis 2–4 mm diam.
28a. Leaves thin, chartaceous, slightly lustrous, the ultimate venation prominent and raised on both surfaces, the apex acuminate; orifice of gynoecious flower 3–4 mm diam. (ca. ½ total width of receptacle); androecious buds globose; Madagascar ..... 32. *T. perrieri*
28b. Leaves subcoriaceous, dull, the ultimate venation frequently obscure on both surfaces, the apex shortly acuminate to mucronate, obtuse, rounded or retuse; orifice of gynoecious flower 1–2 mm diam. (ca. ¼ total width of receptacle); androecious buds obovoid to ellipsoid; Mauritius, dry western forests ..... 33. *T. quadrifida*
27b. Gynoecious receptacle as wide as or wider than long, subglobose to globose-depressed or napiform-depressed; ramiflorous species; inflorescence a slender pleiochasium 20–50 mm long; floral axis 1–1.5 mm diam. (if cauliflorous, then flowers solitary or in fascicles of 2–3).
29a. Floral axis 20–45 mm long; androecious buds distinctly apiculate; Madagascar.
30a. Lamina 34–47 mm by 18–28 mm; stamens 35–36, sessile, obtuse to deltoid, 0.6–1 mm long, the loculi apically confluent into a single crescentiform loculus; orifice of gynoecious flower closed in bud, at anthesis 4-lobed, X-shaped ..... 11. *T. beanjadensis*
30b. Lamina 42–80 mm by 24–34 mm; stamens ca. 200, lanceolate to subulate, 2.5–4 mm long, the loculi separate, lateral; orifice of gynoecious flower open in bud, at anthesis circular, entire ..... 12. *T. madagascariensis*
29b. Floral axis 10–15 mm long (or in the flowers solitary); androecious buds not markedly apiculate; Réunion ..... 13. *T. elliptica*
17b. Mature inflorescence canescent to velutinous-tomentose or strigillose with conspicuous, often fine and ± appressed hairs under dissecting microscope.
31a. Leaves highly lustrous adaxially, dull abaxially; Madagascar ..... 4. *T. nitida*
31b. Leaves not markedly lustrous adaxially, dull on both surfaces; Madagascar, Mauritius, or Comores.
32a. Lamina macrophyllous, ca. 150–325 mm by 85–115 mm; gynoecious flowers in pleiochasia of 6–11, the pedicels 6–23 mm long, the receptacle napiform-depressed, 7–8 mm diam. by 4–5 mm long, the orifice X-shaped, 4(–5)-lobed, the lobes incurved with inner surface bearing 25–40 sterile appendages resembling styles but larger (androecious flowers unknown); Madagascar ..... 7. *T. decaryana*
32b. Leaves smaller, or if as large then floral pedicels 25–60 mm long; female receptacle lobes lacking conspicuous style-like sterile appendages on inner surface (or gynoecious flowers unknown); Madagascar, Mascarenes, Comores.

33a. Androecious and gynoecious floral receptacles with 2–4 low, external longitudinal ridges ..... 9. *T. floricostata*

33b. Androecious and gynoecious floral receptacles lacking 2–4 external ridges (numerous low ribs present in gynoecious flowers of *T. nosybensis*).

34a. Styles bearing long (1–1.5 mm), scattered hairs externally; gynoecious buds and flowers 15–20 mm diam.; Madagascar ..... 8. *T. humbertii*

34b. Styles glabrous or, if bearing scattered hairs, these much shorter, 0.5 mm long (in *T. kirkii*, Anjouan); gynoecious buds and flowers 7–15(–16) mm diam.; Mauritius, Madagascar, Comores.

35a. Androecious receptacle remaining partly or almost completely closed at anthesis, either shallowly split or globose with subentire apical pore; stamens narrowly acute, tapering gradually to a slender, conspicuously prolonged connective; Comores.

36a. Androecious receptacle opening by a small apical orifice ca. 2 mm diam. flanked internally by several series of small, obtuse scale-like tepals; prolonged connectives slightly exserted from orifice; gynoecious flowers unknown; Anjouan. ..... 18. *T. paradoxa*

36b. Androecious receptacle splitting into 3–4 shallow segments, lacking small, obtuse scale-like tepals internally; tips of staminal connectives not exserted from orifice; Anjouan, Mohéli.

37a. Staminal loculi separate; orifice of gynoecious receptacle circular, entire; Anjouan ..... 17. *T. kirkii*

37b. Staminal loculi mostly united basally into a U-shape; orifice of gynoecious receptacle with 4 large deltoid lobes; Mohéli ..... 19. *T. moheliensis*

35b. Androecious receptacle splitting more than halfway open, the lobes spreading flat or reflexing at anthesis, the staminal connectives only slightly or not prolonged (except in *T. moheliensis*); Mauritius, Madagascar, Comores.

38a. Mature floral pedicels 25–80 mm long.

39a. Lamina 250–430 mm by 80–230 mm; flowers either solitary, fasciculate, or in short pleiochasia of 3–7; androecious flowers at anthesis 14–18 mm diam.; stamens 1–1.5 mm long, the loculi apically confluent; slender, basally cauliflorous treelets; Mauritius ..... 25. *T. amplifolia*

39b. Lamina generally much smaller; flowers in ample pleiochasia or thyrses of 7–34; androecious flowers at anthesis 20–35 mm diam.; stamens 2–3 mm long, the loculi separate (apically confluent in *T. bathiei*, Madagascar); larger trees; Madagascar, Comores.

40a. Orifice of gynoecious floral receptacle circular, entire, open even in bud; androecious buds 6–8 mm diam.; Mayotte (Comores) ..... 16. *T. leptophylla*

40b. Orifice of gynoecious floral receptacle closed in bud, at anthesis splitting into a 4-lobed, X-shaped orifice with deltoid lobes; Comores, Madagascar.

41a. Gynoecious buds and flowers externally corky brown, napiform, the apex strongly depressed; lamina 120–220 mm by 40–70 mm; Mohéli (Comores) ..... 19. *T. moheliensis*

41b. Gynoecious buds and flowers externally fulvous velutinous-canescent, globose, the apex apiculate; lamina 40–58 mm by 20–25 mm; Madagascar ..... 31. *T. bathiei*

38b. Mature floral pedicels 5–15 mm long.

42a. Leaves small, 14–45 mm by 9–22 mm, coriaceous, obovate, elliptic or oblong, the apex obtuse to retuse; inflorescence puberulent or sparsely canescent; montane forests of central Madagascar ..... 10. *T. parvifolia*

42b. Leaves much larger, generally exceeding 50 mm long, if apex retuse or obtuse, then inflorescence villous-tomentose; Madagascar, Comores.

43a. Gynoecious receptacle open even in bud, the orifice circular and entire; Comores.

44a. New stems and leaves glabrous; inflorescence a short pleiochasium of 4–9 flowers; mature androecious buds 9–14 mm diam.; stamens 125–150; gynoecious flowers and fruit with short, bluntly columnar styles ca. 0.5 mm long; gynoecious floral orifice ca. ½–⅔ total diam. of receptacle; fruit smooth, mottled reddish brown, the orifice ca. ⅓–½ total diam. of receptacle; Grande Comore ..... 15. *T. comorensis*

44b. New stems and leaves finely pubescent; inflorescence a lax pleiochasium or thyrse of (5–)7–25 flowers; mature androecious buds 6–8 mm diam.; stamens ca. 80–90; gynoecious flowers and fruit with sharply acute, conical styles ca. 0.6–1 mm long; gynoecious floral orifice ca. ¼–⅓ total diam. of receptacle; fruit uniformly dull, corky brown, the orifice ca. ⅙–¼ total diam. of receptacle; Mayotte ..... 16. *T. leptophylla*

43b. Gynoecious receptacle closed in bud, at anthesis splitting into 4 shallow lobes, the orifice X-shaped; Madagascar.

45a. Apex of lamina shortly acuminate to obtuse or retuse; gynoecious receptacle subglobose to napiform, not ribbed externally, the styles 1–1.5 mm long, strongly papillose in flower and fruit; stamens with a very short, apiculate connective; Madagascar ..... 5. *T. hildebrandtii*

45b. Apex of lamina long acuminate; gynoecious receptacle discoid, externally many-ribbed, the styles ca. 0.4–0.6 mm long, not papillose; stamens with an acute, prolonged connective ca. 0.5 mm long; Nosy-Be island (NW Madagascar) ..... 6. *T. nosybensis*

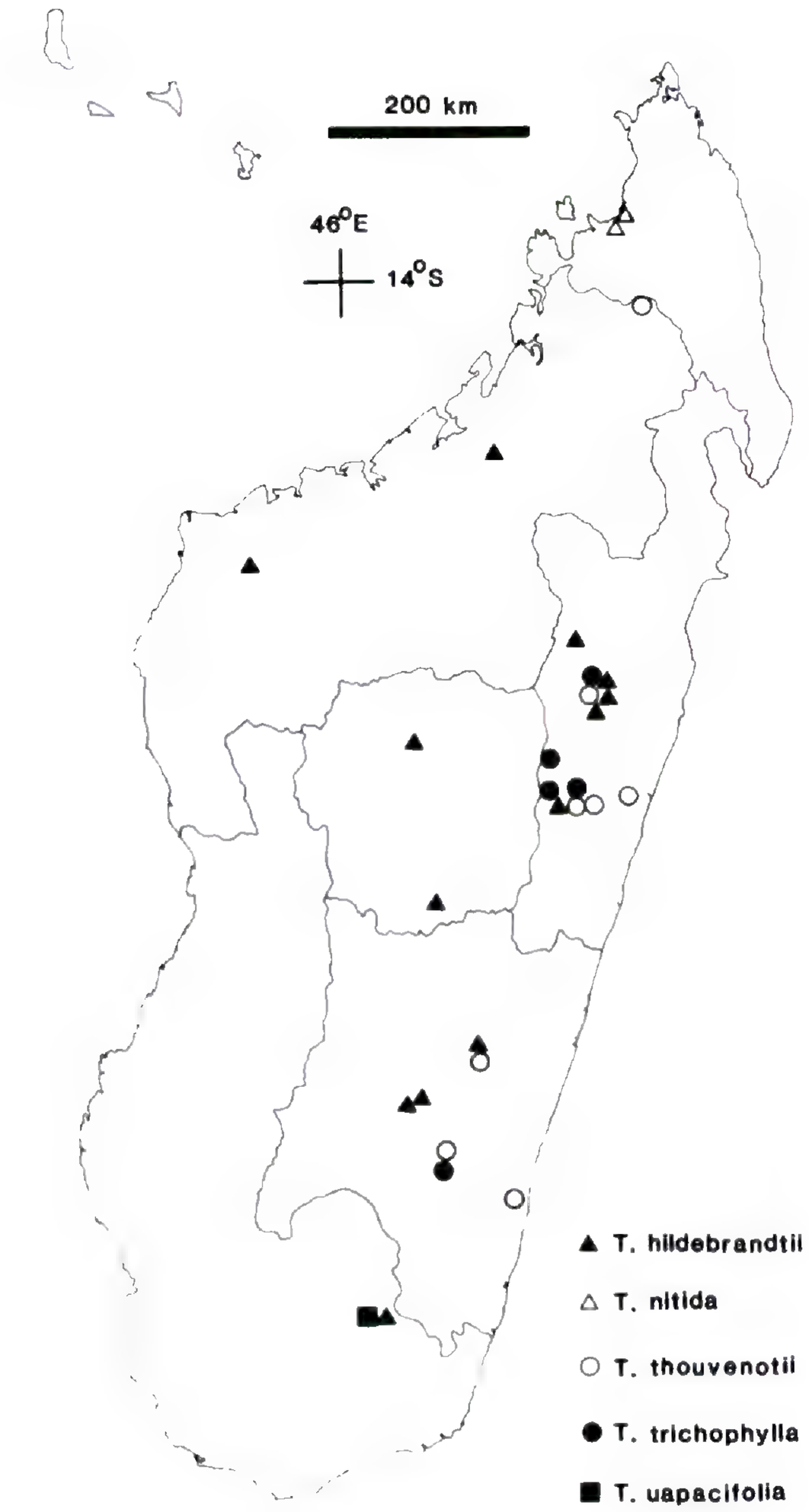


FIGURE 27. Distribution map of some *Tambourissa* species in Madagascar.

(K, syntype); Dec. 1883 (st), *Baron 2243* (K); (fl), *Baron 2994* (BM, K); 1885 (fl), *Baron 3433* (K); Feb. 1882 (st), *Parker s.n.* (K).

Tambourissa trichophylla and its close ally, *T. thouvenotii,* are both characterized by apically dentate adult leaves. This character may represent a state of neoteny, as it occurs in young plants and sucker shoots of many other *Tambourissa* species. *Tambourissa trichophylla* is distinguishable from *T. thouvenotii* by its narrower oblong leaves with fewer and broader teeth (only 1–3 pairs), its more widely spaced secondary veins with lower, stronger arches, its sparser and more curved trichomes, and its smaller flowers with much shorter pedicels and longer bracteoles. Both species remain distinct where they occur sympatrically and both belong to species Group 1A.

Vernacular name. Ambora saha (Madagascar).

2. Tambourissa thouvenotii Danguy, Bull. Mus. Hist. Nat. (Paris), Ser. 1, 28: 250. 1922. TYPE: Madagascar. Tamatave: Analamazaotra (Perinet), ca. 1919 (fl), *Thouvenot 109* (**lectotype, K, here designated; isolectotypes, P, 2 sheets**).

T. trichophylla Baker var. *thouvenotii* Cavaco in Humbert, Fl. Madagascar 80: 25, fig. VII:1–4. 1959.

Monoecious or subdioecious treelet or tree 8–22 m tall and 15 cm or more D.B.H., the new growth densely velutinous, the trichomes simple, yellowish, the mature leafy stems velutinous, 3–5 mm diam. (sucker stems to 12 mm diam.). Leaves opposite, petiolate; petioles velutinous, 10–20 mm by 2–3 mm; lamina subcoriaceous, broadly elliptic to elliptic, rarely broadly oblong, ovate or obovate, (70–)85–185 mm by (37–)50–90 mm, the apex shortly acuminate, rarely obtuse, the base obtuse to rounded, the young lamina adaxially pilose, glabrescent except on costa and major veins, abaxially densely velutinous with soft, straight yellowish hairs, the secondary veins 4–7 pairs, making a 35–50° angle with the costa, the arches high and narrow, the venation obscure adaxially and visible to 2°, prominent abaxially and visible to 4°, the margin slightly thickened and revolute, ciliate, the apical ⅓–⅔ of the lamina usually serrate-dentate with 1–8 pairs of short teeth. Inflorescence cauliflorous, ramiflorous or axillary, a sexually mixed or unisexual pleiochasium of 3–7 flowers, or the flowers rarely solitary, the floral axis velutinous, 25–57 mm by 2–3 mm, subtended by several velutinous, deltoid-subulate bracteoles 2–3 mm long. Androecious flower in bud globose, 10–12 mm diam., hirsute-velutinous, apiculate with several minute, velutinous tepals, the pedicel 12–17 mm by 1.5–2 mm; at anthesis deeply 4-fid, 12–25 mm diam., the lobes spreading flat; stamens numerous, ca. 50–100, deltoid-lanceolate to subulate, 3–7 mm long by 1–1.5 mm wide, slightly incurved, the filament short or sessile, the loculi lateral to slightly unilateral, separate, occupying ⅔–¾ total length of the stamen, the connective prolonged apically, acute, the internal receptacle surface pubescent. Gynoecious flower in bud broadly napiform-depressed, 11–13 mm diam. by 6–7 mm long, velutinous, apiculate with several minute tepals, the pedicel 6–10 mm long; at anthesis shallowly and irregularly 5–6-lobed,

the orifice 3–4 mm diam., the lobes incurved, not reflexed; styles numerous, ca. 100–150, very shortly conical, 0.3 mm long by 0.2 mm wide basally, the apex acuminate to acute, the internal receptacle surface velutinous between the styles. Fruiting receptacle solitary on old branches, irregularly cupuliform, 40–100 mm diam. by 32–55 mm long, the walls 12–18 mm thick, both surfaces corky, reddish brown, externally hirsute-velutinous, the orifice subentire, comprising ¼–½ total width of the fruit; styles numerous, shortly conical, 0.3–1.6 mm long by 0.3–0.5 mm wide basally; pedicel and peduncle 15–50 mm long by 9–15 mm wide. Mature carpels 15–16 mm long, 6–7 mm wide, 4–5 mm thick, the endocarp light brown, the surface scrobiculate.

Distribution. Endemic to Madagascar (Fig. 27).

Habitat. Tambourissa thouvenotii is fairly widespread and often locally common in the *Tambourissa/Weinmannia* montane wet forest zone of the eastern and central regions from ca. 800 to 1,400 m. In addition to the obvious morphological differences, both *T. thouvenotii* and *T. trichophylla* appear to occur sympatrically in at least some areas, e.g., Massif d'Andringitra (*Anon. sub Herb. Alaotra 2242,* MAD; *Anon. sub Herb. Alaotra 2311,* MAD), where they remain distinct.

MADAGASCAR. MAJUNGA: Circagri Bealanana (near Tsaratanana massif), June 1953 (st), *Anon. sub Agronomic Service s.n.* (MAD). FIANARANTSOA: Ampamherana, Fianarantsoa, 24 Nov. 1949 (fl), *Anon. sub SF 1248* (MAD); Andringitra Massif, Ambatapaiso near Antsirabe (sic), 12 Jan. 1945 (st), *Anon. sub Herb. Alaotra 2311* (MAD); in rain forest, Tsararano, Vondrozo district (E coast, near Farfangana), Dec. 1963 (fl), *Bosser 18583* (MAD). TAMATAVE: Ranomafana East, 300–400 m (fr), *Chebonis s.n.* (MAD); Analamazaotra Forest (near Perinet), Jan. 1919 (fl), *Anon. sub SF 73* (probably a syntype, MAD); National Route no. 2 at 1 km W of Perinet, ca. 900 m, 29 Oct. 1978 (st), *Lorence 2014* (MAD, MAU, MO); (st), *Lorence 2015* (MAD, MAU, MO); Perinet, 950 m, 13 Aug. 1968 (st), *McWhirter 121* (K); Analamazaotra, (fl), *Thouvenot 73* (K, P, syntypes); 1919 (fl), *Thouvenot s.n.* (BM); Andovoranto Province, Moramanga District, Analamazaotra Forest, 950 m, 3 Nov. 1912 (st), *Viguier & Humbert 1106* (G); Ambatondrazaka (fl), *Anon. sub SF 2548* (MAD). WITHOUT PRECISE LOCALITY: North Madagascar, 1892 (fr), *Baron 6721* (K).

Tambourissa thouvenotii seems most closely related to *T. trichophylla,* which also possesses dentate-serrate adult leaves. It is distinguishable from the latter species by its much larger, broader and usually elliptic leaves with more numerous teeth (up to 8 pairs) and more closely spaced secondary veins with higher and weaker arches showing a tendency to become almost craspedodromous (Fig. 7A). *Tambourissa thouvenotii* also has a denser, more yellowish indument of straight hairs, much longer floral pedicels, shorter bracteoles, and larger flowers than does *T. trichophylla.* Both species are closely allied to *T. uapacifolia* which also belongs to species Group 1A.

Vernacular names. Ambora, Ambora beravina (Madagascar).

3. Tambourissa uapacifolia Cavaco, Bull. Mus. Hist. Nat. (Paris), Ser. 2, 29: 351. 1957; Cavaco in Humbert, Fl. Madagascar 80: 24, fig. V:6–7. 1959. TYPE: Madagascar. Tulear: upper basin of the Mandrare River (SE), pass and summit of Marosoui, 1,000–1,400 m, 14–15 Nov. 1928 (fl, fr), *Humbert 6604* (holotype, P; isotypes, P, 2 sheets).

Monoecious tree, the new growth densely velutinous, the mature leafy stems 4–5 mm diam., velutinous-hirsute. Leaves opposite to subopposite, petiolate; petioles 5–16 mm by 1.5–2.5 mm, velutinous; lamina subcoriaceous, obovate to elliptic, 65–155 mm by 20–85 mm, hirsutulous when young, later glabrescent except abaxially on the major veins and margin, the apex obtuse or rarely shortly acute, the base acutely cuneate, rarely obtuse, the secondary veins 4–6 pairs, making a 40–50° angle with the costa, the venation depressed and visible to 3° adaxially, raised and visible to 4° abaxially, the margin thickened, slightly revolute, ciliate. Inflorescence cauliflorous or ramiflorous on leafless nodes, a velutinous, pendulous unisexual (always?) pleiochasium of 5–9 flowers, the floral axis 20–55 mm by 1.5–2 mm, subtended by small, naviculate bracteoles 1.5–2 mm long. Androecious flower in bud globose, 6–10 mm diam., velutinous, apiculate, the apex with several pairs of small, hirtellous-velutinous tepals, the pedicel velutinous, 10–17 mm by 1–1.5 mm; at anthesis 4-fid; 17–20 mm diam., stamens ca. 100–300, clavate, 1–2 mm long by 0.6–1 mm wide, the filament comprising ca. ⅓–½ the total length, the loculi lateral, separate or confluent apically, ± parallel, comprising ca. ½–⅔ total length of the stamen, the connective not prolonged, the external surface of loculi bearing medially several scattered simple hairs, the internal receptacle surface bear-

ing scattered simple hairs between the stamens. Gynoecious flower unknown. Fruiting receptacle solitary on older leafless stems, the submature fruit cupuliform, 35–41 mm diam. by 20–27 mm long, the orifice ca. 10–15 mm diam., subentire, the walls 14–16 mm thick, externally pale corky brown with scattered hairs, the internal surface hirsute, the styles scattered, broadly conical, 0.5–0.6 mm long by 0.6–0.8 mm wide basally; pedicel and peduncle hirsute-velutinous, 25–50 mm long by 3–4 mm diam.; submature carpels 9–12 mm long, 7–8 mm wide, 5–6 mm thick, the endocarp light brown, the surface foveolate.

Distribution. Endemic to Madagascar (Fig. 27).

Habitat. *Tambourissa uapacifolia* is currently known from three collections. The type is from southeastern Madagascar at 1,000 to 1,400 m, presumably in *Tambourissa/Weinmannia* wet forest where Humbert also collected *T. capuronii* and *T. hildebrandtii*. The other two collections are from near Moromanga, probably in the same vegetation type. Additional collections and field data are obviously needed.

MADAGASCAR. TAMATAVE: S of Moromanga, 9 Feb. 1930 (fl), *Decary 7042* (P); Moromanga to Andasibe (Perinet), pk 51, 26 Oct. 1953 (fr), *Anon. in SF-7805* (P).

Tambourissa uapacifolia belongs to species Group 1A, which also includes *T. trichophylla* and *T. thouvenotii* (for which Humbert apparently mistook it). It is distinguishable from the previous two species by its larger and laxer inflorescence with longer floral pedicels, smaller bracteoles, stamens with scattered hairs on the loculi, unprolonged connectives, and by its obtuse leaves with entire margins resembling those of certain species of *Uapaca* (Euphorbiaceae).

4. Tambourissa nitida Danguy, Bull. Mus. Hist. Nat. (Paris), Ser. 1, 34: 280. 1928; Cavaco in Humbert, Fl. Madagascar 80: 25. 1959. TYPE: Madagascar. Diego Suarez: S of Biramanja (Ambilobe), ca. 1927 (fl, fr), *Ursch 267* (holotype, P; isotype, P).

Small tree attaining 6 m tall, the new growth pilose-hirsute, the mature leafy stems 1.5–4.5 mm diam., blackish brown, hirsutulous. Leaves glabrous, opposite, petiolate; petioles 10–16 mm by 1–1.5 mm; lamina chartaceous to subcoriaceous, ovate to narrowly ovate, elliptic, rarely oblong, 60–110 mm by 26–40 mm, the apex long acuminate, ± recurved, the base acutely decurrent, the secondary veins 6–9 pairs, making a 60–70° angle with the costa, the venation prominent on both surfaces, visible to 3° adaxially and to 4° abaxially, the adaxial surface highly lustrous, the abaxial surface dull, the margin slightly revolute. Inflorescence axillary, a sexually mixed pleiochasium of 3–5 flowers, or the flowers solitary, the axes hirsute-canescent with pale, simple hairs; floral axis 5–12 mm by 1 mm, subtended by several subulate-naviculate, hirsute bracteoles 1.5–2 mm long. Androecious flower in bud globose, 6–7 mm diam., sparsely pubescent, apiculate with 3–4 narrowly deltoid, hirsute tepals, the pedicel 3–4 mm by 1–1.5 mm, subtended by a bracteole; androecious flower at anthesis unknown; stamens in bud ca. 60, ellipsoid to clavate, 1–1.5 mm long by 0.5 mm wide, the loculi separate, lateral, occupying ca. ½ total length of the stamen, connivent at the obtuse apex, the connective not prolonged, the internal receptacle surface with scattered groups of simple hairs between the stamens. Gynoecious flower at anthesis unknown, in bud turbinate or napiform, 6.5–8 mm diam. by 4–5 mm long, usually with two low, basal longitudinal ridges, externally hirsutulous-canescent, apiculate with 3–4 acute tepals; styles numerous, ca. several hundred, conical or clavate, 0.7–0.9 mm long by 0.3 mm diam., medially ventricose, the apex abruptly acuminate, the internal receptacle surface velutinous, the hairs slightly shorter than the styles. Mature fruiting receptacle unknown. Immature malformed fruit axillary on the leafy stem, ± napiform, ca. 15 mm diam., externally blackish and corky brown, pubescent, the internal surface hirsute, the scattered styles broadly conical, tapering to an acuminate apex, 0.5–0.6 mm wide by 0.8–1 mm long; pedicel and peduncle stout, obconical, 10–12 mm long by ca. 5 mm diam. medially. Carpels unknown.

Distribution. Endemic to Madagascar (Fig. 27).

Habitat. *Tambourissa nitida* is only known from two collections, both from the Sambirano region of Diego Suarez near the northern tip of Madagascar. The area where both collections originated appears to represent a transition zone between wet and deciduous forest.

MADAGASCAR. DIEGO SUAREZ: Ifazy Valley, Aug. 1909, *Perrier de la Bâthie 10126* (P).

Tambourissa nitida belongs to species Group

1B. Although the slight ridges on the female receptacles are reminiscent of *T. floricostata, T. nitida* is easily distinguishable because of its adaxially lustrous leaves with long acuminate, recurved apices. Also, its gynoecious flowers are more densely velutinous internally and its stamens lack the prolonged connectives of most allied species. Mature flowers, fruiting receptacles, as well as the habitat of this remarkable species are unknown.

5. Tambourissa hildebrandtii Perk. in Perk. & Gilg, Pflanzenr. 4, 101: 69, fig. 18:N–P. 1901; Perk., Gatt. Monim. fig. 34:N–P. 1925; Cavaco in Humbert, Fl. Madagascar 80: 29. 1959. TYPE: Madagascar. Tananarive: North Betsileo (Ant-) Sirabe, Aug. 1880 (fl), *Hildebrandt 3563* (lectotype, K, here designated; isolectotypes, BM; G, 2 sheets; P, 2 sheets).

T. baroni Drake in Grandidier, Hist. Phys. Madagascar 1(1): 24. 1902; Perk., Pflanzenr. 4, 101 (Nachtr.): 41. 1911; Cavaco, Bull. Soc. Bot. France 104: 284, figs. 2, 5. 1957; Cavaco in Humbert, Fl. Madagascar 80: 26, fig. VII:5–7. 1959. TYPE: Central **Madagascar. Without precise locality (ca. 1890),** *Baron 2954* (lectotype, K, here designated; isolectotype, P).

T. quadrifida sensu Drake in Grandidier, Hist. Phys. Madagascar 1(1): 21. 1902, pro parte, non Sonn.

Monoecious tree attaining 10 m tall and 30–40 cm D.B.H., the bark thin, gray, flaking, the new growth villous to velutinous with straight or matted simple hairs, the mature leafy stems 1.5–3 mm diam., dark brown, villous, glabrescent. Leaves opposite to subopposite, petiolate; petioles villous-hirsute, 4–12 mm by 1–1.2 mm; lamina chartaceous to subcoriaceous, sparsely pilose abaxially, more densely so along the costa and major veins, adaxially glabrescent, ovate, elliptic to narrowly elliptic, oblong or narrowly oblong, lorate or rarely obovate, 40–115(–135) mm by 17–44 mm, the apex shortly acuminate, shortly acute, obtuse or emarginate, the base acute to obtuse, sometimes slightly decurrent, the secondary veins 4–9 pairs, making a 55–80° angle with the costa, the venation visible to 2(–3°) adaxially, to 3(–4°) abaxially, the margin thickened, slightly revolute. Inflorescence terminal, axillary or ramiflorous, cinereous, velutinous-tomentose, a unisexual or sexually mixed pleiochasium of 3–7(–9) flowers, usually terminated by a single gynoecious flower, the floral axis 5–30 mm by 1.2–2 mm, the axis and pedicels subtended by naviculate-subulate bracteoles 1–3.5 mm long. Androecious flower in bud finely cinereous-tomentose, globose to globose-depressed, 6–7 mm diam. by 5–6 mm long, apiculate with 4 narrowly acute tepals ca. 1 mm long, the pedicel 8–10 mm by 0.6–1 mm; at anthesis deeply 4-fid, 15–18 mm diam., the lobes spreading flat; stamens ca. 75–90, deltoid to ovoid-ellipsoid, slightly recurved, 1.2–2 mm long by 0.8–1.2 mm wide, the loculi ± unilateral, introrse, separate, occupying ⅔–¾ total length of the stamen, the filament subsessile, the internal receptacle surface with scattered to dense simple hairs between the stamens. Gynoecious flower in bud subglobose-napiform, more densely tomentose than androecious flower, apiculate with 4 acutely deltoid tepals, the pedicel 10–15 mm by 1–1.2 mm; at anthesis 7–9 mm diam. by 5–6 mm long, the orifice X-shaped, 3–3.5 mm diam., splitting into 4 deltoid, suberect to outcurved lobes; styles numerous, ca. 150–200, narrowly conical, 1–1.5 mm long by 0.4–0.6 mm wide basally, the surface strongly papillose, the internal receptacle surface densely velutinous-tomentose between the styles. Fruiting receptacle usually solitary on leafless stems, ± shallowly cupuliform, 30–50 mm diam. by 20–35 mm long, the cavity shallow to almost absent, the external surface pale, mottled corky brown, the orifice comprising ⅓–½ total width of the fruit, subentire, the walls 15–25 mm thick, the internal surface with scattered, narrowly conical papillose styles 0.5–0.7 mm long by 0.5 mm wide basally, interspersed with scattered to dense hairs; pedicel and peduncle tapered, to 55 mm long by 4–5 mm diam. medially. Mature carpels 7–8 mm long, 4–5 mm wide, 3–4 mm thick, ovoid-compressed, the endocarp light brown, the surface scrobiculate.

Distribution. Endemic to Madagascar (Fig. 27).

Habitat. *Tambourissa hildebrandtii* displays a wide ecological amplitude comparable to that of *T. purpurea.* It ranges from the *Tambourissa/Weinmannia* montane wet forest zone above 800 m in the eastern region, to montane forests of the central plateau (ca. 1,000–1,400 m) and extends to the dry semideciduous forests of the western domain where it finally disappears.

MADAGASCAR. FIANARANTSOA: Fianarantsoa (fr), *Anon. sub SF 2145* (MAD); Inselbergs W of Ambalavao, at Pk 475, 970 m, 31 Jan. 1975 (fl, fr), *Croat 30194* (MAD, MO); National Route no. 7 at 11 km

W of Ambalavao, 950 m, 5 Nov. 1978 (fl, fr), *Lorence 2043* (MAD, MAU, MO). MAJUNGA: Natural reserve no. 8, Namoraka (Saolala), 7 Feb. 1951 (fr), *Anon. sub RN 3298* (MAD). TAMATAVE: Ambatondrazaka (near Lake Alaotra) (fl, fr), *Anon. sub. SF 1723* (MAD); Ambohijanahary, 1,000 m (by Lake Alaotra), 5 Jan. 1945 (fl), *Anon. sub SF 2188* (MAD); small forest at Marovato, East Manaka (near Lake Alaotra), 13 Nov. 1946 (fl), *Anon. sub Herb. Alaotra 3102* (MAD, 2 sheets); Didy Forest, Ambatondrazaka (near Lake Alaotra), ca. 1,200 m, 5 July 1952 (st), *Anon. sub SF 5498* (MAD); 2 June 1952 (fl), *Botoalma sub SF 4145* (MAD, 2 sheets); Andevorante, Moramanga, 5 Oct. 1912 (fl), *Afzelius s.n.* (K). TANANARIVE: Finoarive, 1,400–1,600 m, 18 Mar. 1930 (fl, fr), *Decary 7633* (K, 2 sheets); Bongolave, 800–900 m, Tsiroanandidy, July 1974 (fr), *Morat 4608* (MAD). TULEAR: upper basin of the Mandrare River (SE), pass and summit of Marosoui, 1,000–1,400 m, 14–15 Nov. 1928 (fr), *Humbert 6606* (B). PROVINCE UNCERTAIN: Arkotreano, forest N of the road to Nickelville, 29 Dec. 1944 (fl, fr), *Anon. sub Herb. Alaotra 2091* (MAD, 2 sheets); Menavavakely, Mevatanana, 16 Apr. 1951 (fl), *Anon. sub SF 3588* (MAD). WITHOUT PRECISE LOCALITY: Central Madagascar, Jan. 1882 (fr), *Baron 1144* (K, P, syntypes of *T. baroni*); (fl), *Baron 2417* (K, P); 1883 (fl), *Baron 2477* (K).

Tambourissa hildebrandtii belongs to species Group 1B and is distinguishable from other members of the group, notably its closest ally, *T. nosybensis,* by its strongly papillose styles, fruiting receptacle with a very small to almost nonexistent central cavity, and its villous stems. The type of *T. baroni* has fewer flowers and smaller, more obtuse leaves than that of *T. hildebrandtii,* but easily falls within the range of variation displayed by the species. A comparable degree of variation in leaf size and shape frequently occurs on a single individual (e.g., *Lorence 2043,* MAD, MAU, MO).

Fresh flowers of *Tambourissa hildebrandtii* are externally grayish green to peach colored. The gynoecious flowers have purple styles, whereas the androecious flowers are beefy red within and produce a sweet, fruity odor. In mixed inflorescences, anthesis occurred in gynoecious flowers before it occurred in androecious flowers (*Lorence 2043*).

Vernacular names. Ambora, Ambora saha (Madagascar).

Monoecious to subdioecious tree 6 m tall, the bark pale gray, licheniferous, longitudinally fissured, the new growth pilose with short, fulvous hairs, the mature leafy stems terete, 2–3.5 mm diam., brown, pilosulous. Leaves opposite, petiolate; petioles 6–11 mm by 1–1.2 mm, pilosepubescent; mature lamina adaxially glabrescent, abaxially sparsely hirsutulous, especially along the costa and major veins, brown, discolorous, subcoriaceous, narrowly elliptic to narrowly oblong, occasionally ± falcate, 60–125 mm by 20–36 mm, the apex acuminate, the base acutely cuneate, the secondary veins 4–6 pairs, making a 35–45° angle with the costa, the intersecondary and tertiary branches straight with strong admedial orientation, ± perpendicular to the costa, the venation visible to 2(–3°) adaxially, and to 3(–4°) abaxially, the margin slightly revolute, thickened. Inflorescence cauliflorous, moderately to densely fulvous velutinous, a unisexual or rarely sexually mixed pleiochasium of 9–12 flowers, the floral axis 50–87 mm by 2 mm, the pedicel and peduncle 7–20 mm by 1–2 mm, the joint swollen, subtended by a caducous, subulate-naviculate bracteole 1–2 mm long. Androecious flower in bud unknown; at anthesis deeply 5-fid, 17 mm diam., the lobes thick, spreading flat, the receptacle externally hirsute; stamens ca. 70, incurved, ovoid-acuminate, subsessile, 1.5–2 mm long by 0.7–1 mm wide, the loculi lateral, separate, the connective acute, prolonged for ca. 0.5 mm, the internal receptacle surface with rare, scattered hairs among the stamens; pedicel ca. 2 mm diam. Gynoecious flower in bud discoid-patelliform, 9–10 mm diam. by 3–4 mm long, longitudinally multi-ribbed, velutinous, the apex depressed, with 4 subulate tepals ca. 1 mm long, the pedicel 9–20 mm by 1–1.2 mm; at anthesis splitting apically into 4(–6) short, straight or incurved deltoid lobes, the orifice small, X-shaped; styles numerous, ca. 400, broadly conical to columnar, apiculate, 0.4–0.6 mm long by 0.4–0.5 mm diam. basally, not papillose, the internal receptacle surface velutinous between the styles. Fruiting receptacle unknown. Figure 28.

6. Tambourissa nosybensis Lorence, Bull. Mus. Hist. Nat. (Paris), Ser. 4, Sect. B, Adansonia 3(3): 302, pl. 3, figs. 12, 13. 1982. TYPE: Madagascar. Diego Suarez: Nosy Be Island (Nossi-Bé); Lokobe, Natural Reserve no. 6, 350 m, 12 Dec. 1967 (fl), *Bernardi 11847* (holotype, G; isotypes, K, P, Z).

Distribution. Known only from Nosy Be Island off the northwestern coast of Madagascar (Fig. 29).

Habitat. Tambourissa nosybensis was collected in depauperate lower montane wet forest (presumably of Chlaenaceae, Myristicaceae, and *Anthostema*) at 350 m.

FIGURE 28. *Tambourissa nosybensis* Lorence.—A. Habit.—B. Androecious flower at anthesis.—C. Stamen, abaxial view.—D. Gynoecious inflorescence at anthesis.—E. Gynoecious flower at anthesis, apical view.—F. Gynoecious flower at anthesis, longitudinal section.—G. Styles, longitudinal section. All *Bernardi 11847* (G). Bars equal 10 mm in A, B, D, E, and 1 mm in C, F, G.

FIGURE 29. Distribution map of some *Tambourissa* species in Madagascar.

MADAGASCAR. WITHOUT PRECISE LOCALITY: ca. 1883 (fl), *Humbolt 642* (K, P).

Tambourissa nosybensis belongs to species Group 1B. Although most closely allied to *T. hildebrandtii* (for which Bernardi mistook it), *T. nosybensis* possesses sufficient distinguishing characters to merit specific status (Table 15). These include a number of specialized features, notably the production of a mucilaginous exudate in the mature gynoecious flowers (conspicuous in rehydrated flowers), and also an apparent trend towards dioecy. I first thought the species was dioecious but then found a single androecious flower among some 34 gynoecious flowers, suggesting it is monoecious. Further collections, particularly of androecious flowers and fruit, and observations on the biology of this interesting species are required.

7. **Tambourissa decaryana** Cavaco, Bull. Mus. Hist. Nat. (Paris), Ser. 2, 29: 287. 1957; Cavaco in Humbert, Fl. Madagascar 80: 22, fig. VI:1–4. 1959. TYPE: **Madagascar. Tamatave: Mt. Vatovavy (Mananjary), 22 Nov.** 1938 (fl, fr), *Decary 13697* (holotype, P).

Cauliflorous tree 10–16 m tall, possibly dioecious (?), the new growth pilose-strigillose, the adult leafy stems terete, pilose, 4–5 mm diam. Leaves opposite, petiolate; petioles 15–20 mm by 2–4 mm, pilose; lamina subcoriaceous, oblong, 150–325 mm by 85–115 mm, adaxially glabrous, abaxially strigillose with white, appressed hairs, the apex acuminate, the base obtuse to rounded, the secondary veins 6–14 pairs, making a 60–70° angle with the costa, the venation prominent, visible to 4° on both surfaces, the margin slightly revolute. Androecious flowers unknown. Gynoecious inflorescence cauliflorous, a fulvous, tomentose or velutinous pleiochasium of 6–11 flowers, the floral axis (10–)30–135 mm by 1.5–3 mm, subtended basally by several deltoid-naviculate bracteoles ca. 1 mm long, the pedicel 6–23 mm by 1–1.5 mm, subtended by a velutinous subulate bracteole (1–)4–5 mm long. Gynoecious flowers in bud napiform-depressed, 7–8 mm diam. by 4–5 mm long, externally tomentose to velutinous, the apex apiculate with 4–5 minute velutinous tepals; at anthesis 8–11 mm diam. by 7–8 mm long, the orifice shallowly 4–5-fid, comprising ½–¾ total width of the receptacle, the lobes suberect, the margins thickened; styles numerous, ca. 200–300, shortly conical, 0.4–0.5 mm long by 0.2–0.3 mm wide, basally ± ventricose, the apex acute, slightly papillose, the ovule amphitropous; receptacle lobes bearing internally several series of larger, sterile, hirsutulous conical appendages (ca. 25–40), these 1–1.5 mm long by 0.5–0.8 mm diam., the internal receptacle surface densely velutinous between the styles and on the lobes. Fruiting receptacle produced on the trunk and branches, cupuliform, 40–50 mm long by 50–70 mm diam., externally corky, the orifice comprising ⅕–⅓ total width of fruit, the styles conical, 0.5 mm long, interspersed with hairs; pedicel and peduncle 37–110 mm by 6–9 mm.

Distribution. Endemic to Madagascar (Fig. 29).

Habitat. Tambourissa decaryana occurs in the lower altitude Myristicaceae/*Anthostema* wet forest zone in the eastern domain, from ca. 250 to 500 m.

TABLE 15. Some distinguishing morphological features of *Tambourissa hildebrandtii* and *T. nosybensis*.

Character	*T. hildebrandtii*	*T. nosybensis*
Angle of secondary veins to costa	55–80°	35–45°
Intersecondary veins and tertiary branches	zig-zag, weak admedial orientation	straight, strong admedial orientation
Inflorescence position	ramiflorous or axillary	cauliflorous
Inflorescence pubescence	cinereous, hirsute, or tomentose	fulvous, velutinous
Stamens	outcurved	incurved
Loculi	unilateral	bilateral
Connective	short, obtuse, or absent	acute, 0.5 mm long
Gynoecious receptacle	subglobose-napiform, not longitudinally ribbed	discoid-patelliform, longitudinally ribbed
Orifice lobes	4, suberect to everted	4(–6), incurved or straight
Styles	narrowly conical, 1–1.5 mm long, strongly papillose	broadly conical to columnar, apiculate, 0.4–0.6 mm long, not papillose
Ovule	anatropous, pendulous	amphitropous, oblique
Mucilaginous exudate	absent	present, covering styles
Tanniferous cells	present	absent
Stone cells	absent	present

MADAGASCAR. TAMATAVE: Mt. Vatovavy, Mananjary Bassin, 250 m, Aug. 1911 (fr), *Perrier de la Bâthie 10091* (P); Marolambo District, Andonabe Canton, near Ambatomitsangana, 16 Sept. 1963 (fr), *Anon. in SF-21357* (P); Ambodiriana (R.N. 1), 250–500 m, 21 Aug. 1957 (fr), *Capuron 18111-SF* (P). WITHOUT PRECISE LOCALITY: Feb. 1881 (fl), *Parker s.n.* (K).

Parker s.n. differs from the type of *Tambourissa decaryana* in having a longer, less densely pubescent floral axis, and furthermore has mature gynoecious flowers (*Decary 13697* is mostly in bud). Although *Parker s.n.* lacks leaves, the presence of large sterile appendages within the flowers, an abundance of oil cells in the receptacular ground tissue, amphitropous ovules, and production of mucilage by the styles all correspond well with the type of *T. decaryana*.

The species is characterized by a moderately to densely pubescent inflorescence, long bracteoles, 4–5-fid gynoecious flowers with an X-shaped orifice and suberect lobes, and sparsely pubescent leaves, characters which place it in species Group 1B. Its huge, macrophyllous leaves (assuming they are not from a vigorous sucker shoot) and presence of several rows of large, style-like sterile appendages surrounding the styles set it apart from all other Madagascan species, although *Tambourissa parvifolia* has similar appendages. The sterile appendages in *T. decaryana* resemble the styles but are 2–4 times larger, hirsutulous, and lack an ovule at the base. Numerous oil cells occur in the receptacular ground tissue. The species also displays certain specialized features shared with *T. nosybensis*, i.e., production of a mucilaginous exudate and a tendency towards dioecy.

8. Tambourissa humbertii Cavaco, Bull. Soc. Bot. France 104: 283. 1957; Cavaco in Humbert, Fl. Madagascar 80: 28, fig. IX:1–4 (non fig. VIII). 1959. TYPE: Madagascar. Fianarantsoa: high valley of the Rienana River, Matitanana Basin, 18–24 Nov. 1924 (fl), *Humbert 3593* (holotype, P; isotype P).

Large tree, the new growth velutinous, the mature leafy stems flattened, stramineate, 3.5–6 mm diam., sparsely hirsutulous, glabrescent. Leaves opposite, petiolate; petioles hirsutulous, glabrescent, 10–13 mm by 1.5–2 mm; lamina glabrous, subcoriaceous, elliptic to oblong, 82–126 mm by 35–60 mm, the apex shortly acute, the base acute, slightly decurrent, the secondary veins 6–9 pairs, making a 60–70° angle with the costa, the venation visible to 3° on both surfaces, the margin revolute, the adaxial laminar surface moderately lustrous. Dioecious? Androecious flowers unknown. Gynoecious inflorescence presumably cauliflorous, a fascicle of 2–3 flowers, or a short, 5–17-flowered pleiochasium, the floral axis stout, 30–50 mm long, lenticellar, canescent, the pedicel velutinous-canescent, jointed below the middle, the pedicel and peduncle 12–20 mm by 2–3 mm, with 1 to several velutinous, deltoid-naviculate basal bracteoles 1–2 mm long. Gynoecious flower in bud canescent, broadly

napiform-depressed, 13–15 mm diam. by 5 mm long, apiculate with several minute, coalescent velutinous tepals; at anthesis broadly napiform-discoid to patelliform, 18–21 mm diam. by 6–8 mm long, the orifice X-shaped, ca. 10 mm diam., splitting for ca. ½ the length of the receptacle into 4(–5) suberect, fleshy deltoid lobes, the margins thickened; styles numerous, ca. 500 or more, densely crowded, ovoid-ventricose, 1–1.2 mm long by 0.5–0.7 mm wide basally, the apex shortly acuminate or apiculate, papillose, the surface bearing scattered simple hairs ca. 1–1.5 mm long, the internal receptacle surface velutinous between the styles and on the lobes the numerous short hairs mixed with scattered long hairs. Fruit unknown.

Distribution. Endemic to Madagascar (Fig. 29).

Habitat. *Tambourissa humbertii* is known only from the type collection, presumably from the *Tambourissa/Weinmannia* montane wet forest zone from ca. 1,000 to 1,400 m. Further collections of this striking species, particularly androecious flowers and fruit, and observations on its life history are needed.

In contrast to Cavaco's (1957b) statement that *Tambourissa humbertii* approaches *T. ficus* from Mauritius, I find that it differs from the latter species in several important characters. Most notably it lacks the ternate-whorled to subalternate leaves and tanniferous idioblasts in the floral ground tissue characteristic of *T. ficus*. *Tambourissa humbertii* appears rather to belong to species Group 1B and is distinguishable from other members of the group by its much larger gynoecious flowers and presence of long hairs on the styles. Styles of *T. kirkii* (Group 2B; Comores), incidentally, bear similar but shorter scattered hairs. In addition, the internal surface of the gynoecious receptacle of *T. humbertii* bears mixed long and short hairs, a feature found in no other species.

In spite of their relatively large size, gynoecious flowers of *Tambourissa humbertii* structurally most closely resemble those of *T. decaryana*. In both species the orifice lobe margins are conspicuously thickened and numerous oil cells occur in the ground tissue. Flowers of *T. humbertii* are much larger, however, and lack the peculiar sterile appendages characteristic of the latter species.

9. Tambourissa floricostata Cavaco, Bull. Soc. Bot. France 105: 39. 1958; Cavaco in Humbert, Fl. Madagascar 80: 40, fig. IV:7–11. 1959. TYPE: Madagascar. Tamatave: Analamazaotra forest, Feb. 1919 (fl), *Ramanantoavolana sub T. Thouvenot 134* (holotype, P; isotypes, P, 2 sheets).

Schrameckia madagascariensis Danguy, Bull. Mus. Hist. Nat. (Paris), Ser. 1, 28: 249. 1922 non *Tambourissa madagascariensis* Cavaco, 1957.

Monoecious tree 18–20 m tall, the new growth unknown, the mature growth subglabrous, the mature leafy stems terete, 1.5–2 mm diam. Leaves opposite to subopposite, petiolate; petioles 7–13 mm by 0.8–1 mm; lamina subcoriaceous to coriaceous, glabrous, elliptic to obovate, rarely oblong, occasionally slightly falcate basally, 35–85 mm by 15–36 mm, the apex obtuse to retuse, its extremity usually thickened or apiculate, the base acutely cuneate to acutely decurrent, the secondary veins 4–7 pairs, making a 55–60° angle with the costa, the venation visible to 3° adaxially and to 4° abaxially, the margin thickened, slightly revolute. Inflorescence ramiflorous, a puberulent, sexually mixed pleiochasium of (3–)5–9 flowers attaining 120–160 mm by 60–70 mm, axillary or on leafless nodes, or the flowers solitary and axillary or terminal, the floral axis (17–)23–140 mm by 1–3 mm, ± flattened, often leafy. Androecious flower in bud quadrangular-globose, 9–12 mm diam., with 2–4 prominent longitudinal ridges, apiculate with 4 deltoid-rounded hirsute tepals; pedicels 16–30 mm by 1–1.5 mm, flattened, puberulent, each subtended by a naviculate-deltoid bracteole; at anthesis 4-fid, 25 mm diam., splitting to ca. ½–⅔ total length of the receptacle, the lobes incurved, not spreading, each lobe with ca. 2 fleshy, obtuse scale-like tepals internally near the apex; stamens 16–22, large, ovoid to deltoid, acute, 3–4.5 mm long by 1.5–2.5 mm wide, the loculi lateral, free, the connective broad, ± sessile, the apex apiculate, acute, the internal receptacle surface ± glabrous. Gynoecious flowers solitary and axillary or terminal on the mixed inflorescence, the receptacle globose-depressed, 13–18 mm diam. by 5–7 mm long in bud, with 2 lateral ridges, the orifice small, 1–2 mm diam., flanked by 4 obtuse, decussate tepals; pedicels to 55 mm by 2 mm. Immature fruiting receptacle ca. 47 mm diam., broadly napiform-depressed, the orifice ca. 5 mm diam., subentire, the external surface corky brown, the internal surface with numerous scattered, shortly conical styles ca. 0.5–1 mm long by 0.5 mm wide

basally, the surface between the styles hirsute. Submature fruiting receptacle solitary on leafless stems, shallowly cupuliform, 20 mm long by 45–57 mm diam., externally venose, corky, the pedicel and peduncle tapered, 120–150 mm by 4–5 mm; mature carpels unknown.

Distribution. Endemic to Madagascar (Fig. 29).

Habitat. Known only from three collections, all from the Perinet area (Analamazaotra), in the *Tambourissa/Weinmannia* wet forest zone from ca. 900 to 950 m. *Thouvenot 134* was collected in February with flowers and young fruit. As the Analamazaotra forest is included in a nature reserve, it is probable that *T. floricostata* still occurs there; much intact forest still remained in 1978. However, additional flowering and fruiting collections and data on its life history are needed.

MADAGASCAR. TAMATAVE: Analamazaotra, Feb. 1912 (seed), *Perrier de la Bâthie 10128* (P); Zedsiadra (or Djedsiatsa?) near Perinet (st), *Schedl 40* (MAD).

In spite of the large size and small number of stamens in androecious flowers of *Tambourissa floricostata,* the species possesses a number of attributes which suggest inclusion in species Group 1C, along with *T. parvifolia* (Table 5). It differs from the latter species by its larger leaves, flowers, and receptacles with two to four prominent external longitudinal ridges.

Vernacular names. Ambora, Ambora lahy, Ambora vavy (Madagascar).

10. Tambourissa parvifolia Baker, J. Bot. n.s. 11: 267. 1882; Baillon, Bull. Mens. Soc. Linn. Paris 1: 342. 1882; Perk. & Gilg, Pflanzenr. 4, 101: 70. 1901; Perk., Pflanzenr. 4, 101 (Nachtr.): 42. 1911; Cavaco in Humbert, Fl. Madagascar 80: 36, fig. X:1–4. 1959. TYPE: Madagascar. Without precise locality ("Central Madagascar," probably Tananarive): 1880 (fl), *Parker s.n.* (holotype, K).

T. quadrifida sensu Drake in Grandidier, Hist. Phys. Madagascar 1(1): 21. 1902, pro parte, non Sonn.

Monoecious treelet or tree 5–15 m tall, the new growth sparsely hirsutulous, glabrescent, the mature leafy stems 1.5–3.5 mm diam. Leaves opposite, petiolate; petioles 3–5 mm by 0.7–1 mm; lamina glabrous, coriaceous, elliptic to oblong or obovate, 15–47 mm by 9–22 mm, the apex obtuse to retuse, the base acutely cuneate to obtuse, slightly decurrent, the secondary veins 4–5 pairs, making a 55–60° angle with the costa, the venation obscure adaxially or the 2° veins scarcely visible, abaxially visible to 3°, the margin revolute. Inflorescence ramiflorous on leafless stems, an (always?) unisexual, hirtellous-puberulent pleiochasium of 2–11 flowers, the floral axis 12–70 mm by 1–2 mm, basally bracteolate. Androecious flower in bud globose, 5–6 mm diam., apiculate with several minute, coalescent tepals, the pedicel 6–10 mm by 1–2 mm, subtended by a deltoid, hirsute bracteole 2 mm long by 1 mm wide; at anthesis deeply 4-fid, 17–30 mm diam., the lobes spreading flat, the internal receptacle surface bearing several sterile, columnar appendages near the apex of the lobes; stamens ca. 50–60, ± ligulate, 1–1.5 mm long by 0.6–0.8 mm wide, the loculi lateral, free, parallel, comprising ca. ¾ total length of the stamen, the connective not or only slightly prolonged, the internal receptacle surface glabrous. Gynoecious receptacle at anthesis subglobose to napiform, ca. 9–10 mm diam., externally hirsutulous-pubescent, the orifice small, 4-lobed, X-shaped, comprising ca. ¼ total width of the receptacle, the pedicel 7–14 mm long; styles numerous, ca. 200 or more, conical, ca. 0.5 mm long by 0.5 mm wide basally. Fruiting receptacle solitary or in pleiochasia of 2 or more, the axis to 60 mm by 5 mm, hirtellous, the receptacle shallowly cupuliform to napiform-depressed, 30–95 mm wide by 25–40 mm long, the orifice comprising ca. ¼–½ total width of the receptacle, 8–12 mm wide, subentire with several thick, irregularly deltoid lobes, these bearing a number of sterile, clavate appendages 1–2 mm long on their internal surface, the external receptacle surface irregularly reddish brown with pale corky patches, glabrous or sparsely hirsutulous, the internal surface with numerous conical styles 0.3–0.5 mm long and wide basally with scattered simple hairs in between, the pedicel 10–22 mm by 3.5–6 mm. Carpels 5–13 mm long by 5–9 mm wide by 3–4 mm thick, ovoid-compressed, the endocarp tan, the surface scrobiculate.

Distribution. Endemic to Madagascar (Fig. 29).

Habitat. *Tambourissa parvifolia* is restricted to the sclerophyllous montane forest zone of the central plateau at elevations from ca. 1,400 to 2,000 m.

MADAGASCAR. ANTANANARIVO: E of Antsirabe, 2,000 m, 3–4 Nov. 1928 (fl), *Humbert 6351bis* (P); E slope of Ankaratra, 24–26 Mar. 1958 (fl), *Capuron 18507-*

SF (P). FIANARANTSOA: Andringitra, Imaisoa, 1,500–2,000 m, 28 Oct. 1960 (fl), *Leandri et al. 3393* (P). WITHOUT PRECISE LOCALITY: Central Madagascar, 1855 (fr), *Baron 3864* (BM, K, P); (st), *Baron 4204* (P); (fr), *Baron 4205* (K); (fr), *Baron 6048* (P); (fl), *Parker s.n.* (P, 5 sheets).

The sclerophyllous leaves of *Tambourissa parvifolia* are smallest of any known species of *Tambourissa* and probably represent an adaptation to the high altitude montane habitat. In fact, sclerophylly characterizes the majority of arborescent species occurring in this habitat in Madagascar, which has been termed the "forêt dense sclerophylle de montagne" (Koechlin et al., 1974).

In spite of its extremely reduced leaves, *Tambourissa parvifolia* is best placed in species Group 1C along with *T. floricostata*. It displays a number of specialized trends, including reduced leaves, a tendency towards unisexual inflorescences (and possibly dioecy) and the presence of sterile, style-like appendages on the internal surfaces of the receptacle lobes, a feature shared with *T. decaryana*. *Tambourissa parvifolia* is easily distinguished from *T. floricostata* by its small, obutse or emarginate leaves and slender anther filaments.

Vernacular names. Ambora, Amboravato (Madagascar).

11. Tambourissa beanjadensis Lorence, nom. nov. *Ephippiandra capuronii* Cavaco, Bull. Soc. Bot. France 104: 610. 1957; Cavaco in Humbert, Fl. Madagascar 80: 8, fig. I:10–12. 1959 non *Tambourissa capuronii* Cavaco, Bull. Mus. Hist. Nat. (Paris), Ser. 2, 29: 287. 1957. TYPE: Madagascar. Diego Suarez: Beanjada Massif (N of the Masoala Peninsula), E forest at its upper limits ("forêt des cimes"), ca. 1,100 m, 30 Dec. 1953 (fl), *Capuron 8826 bis-SF* (holotype, P).

Medium-sized monoecious tree, the new growth with rare, scattered hairs, the mature leafy stems glabrous, brown, 1.5–2 mm diam. Leaves glabrous, opposite to subopposite, petiolate; petioles 6–9 mm by 1 mm; lamina chartaceous to subcoriaceous, adaxially lustrous, minutely punctate, elliptic, (23–)34–47 mm by (12–)18–28 mm, the apex abruptly and shortly acuminate, the tip thickened, the base cuneate to broadly cuneate, rarely obtuse, the secondary veins 3–5 pairs, making a 75–85° angle with the costa, adaxially scarcely visible, abaxially prominent, the venation visible to 3° abaxially, the margin entire, slightly revolute. Inflorescence ramiflorous or cauliflorous, solitary or clustered, an apparently unisexual pleiochasium of 3–7 flowers, or the flowers rarely solitary, the floral axis 20–40 mm by 1 mm, pilose when young, glabrescent, subtended by several minute, naviculate bracteoles 1 mm long, the pedicel 3–7 mm by 1 mm, subtended by a minute, obtuse naviculate bracteole ca. 1 mm long. Androecious flower in bud globose, 4 mm diam., glabrous, the apex with 4 sparsely pilose obtuse tepals; at anthesis deeply (3–)4(–5)-fid, 8–10 mm diam., the lobes spreading flat, each bearing internally near the apex a small, scale-like tepal 1 mm wide; stamens ca. 35–36, obtuse to deltoid, 0.6–1 mm long and wide, the filament short or sessile, the loculi confluent apically into a single, crescentiform loculus occupying ⅔ or more of the total length of the stamen, the connective thick, not prolonged, the internal receptacle surface glabrous. Gynoecious flower in bud globose-napiform, ca. 6 mm diam. by 4–5 mm long, glabrous, the apex with 4 minutely puberulent obtuse tepals; at anthesis splitting into an X-shaped orifice ca. 1–2 mm wide, the 4 lobes deltoid, the internal receptacle surface with a pubescent ring near the orifice; styles numerous, ca. 200, shortly and broadly conical, 0.3–0.4 mm long and wide, papillose, producing a mucilaginous exudate, the internal receptacle surface with scattered hairs between the styles, the receptacle wall 1 mm thick. Fruiting receptacle unknown.

Distribution. Endemic to Madagascar (Fig. 30).

Habitat. The species is known only from the type collection from the upper limits of what is presumably mid altitude *Tambourissa/Weinmannia* wet forest on mountainous summits. Further collections and field observations are obviously needed.

Features which immediately place this species in the genus *Tambourissa* are the closed, globose gynoecious floral receptacle with an X-shaped orifice and the conical carpels completely immersed in and fused with the receptacle wall. The broadly deltoid, sessile stamens with a single, crescentiform loculus and presence of tepals on the inner surface of the androecious receptacle lobes occur in a number of other *Tambourissa* species, as previously noted. Pollen of the species, figured by Walker (1976) and presumably taken

from the type, also conforms to that of *Tambourissa* rather than that of *Ephippiandra*.

The small leaves and ramiflorous to cauliflorous, pleiochasial inflorescence of *Tambourissa beanjadensis* resemble those of *T. parvifolia*, which differs by its more coriaceous, obtuse leaves, much larger androecious flowers, and longer stamens with distinct filaments and separate loculi. *Tambourissa beanjadensis* is probably best placed in species Group 2A, however, a diverse series of species from Madagascar, Réunion, and the Comores characterized by their deeply 4-fid androecious flowers which spread flat open and have stamens with unprolonged connectives. Its gynoecious flowers, like those of the two Réunion species in this subgroup (*T. crassa* and *T. elliptica*) are globose-depressed, open by an X-shaped orifice, are nearly glabrous within, and produce a mucilaginous exudate. Both latter species are easily distinguished by their much larger leaves, obtusely columnar styles, and stamens with separate thecae.

FIGURE 30. Distribution map of some *Tambourissa* species in Madagascar.

12. Tambourissa madagascariensis Cavaco, Bull. Soc. Bot. France 104: 283. 1957; Cavaco in Humbert, Fl. Madagascar 80: 30, fig. IX:5–8. 1959. TYPE: Madagascar. Majunga: Natural Reserve no. 4 (Tsaratanana, Ambanja), Mangindrano Canton, Bealanana District, 7 July 1953 (fl), *Rababoto sub R.N. 6028* (holotype, P).

Dioecious (?) tree 5–15 m tall, or a lianescent shrub, the new growth with scattered hairs, glabrescent, the mature leafy stems glabrous, 2–3 mm diam., with longitudinal striations. Leaves glabrous, opposite to subopposite, petiolate; petioles 4–7 mm by 1–1.5 mm; lamina chartaceous, broadly elliptic, 42–80 mm by 24–34 mm, the apex acuminate, the tip ± indurated, the base acutely or rarely obtusely decurrent, the secondary veins 5–7 pairs, making a 60–70° angle with the costa, the venation obscure, visible to 2° adaxially and to 3° abaxially, the margin plane to slightly revolute. Inflorescence ramiflorous, axillary or on leafless nodes, a subglabrous unisexual pleiochasium of 3–9 flowers, sometimes leafy in the terminal portion, the floral axis 20–85 mm by 1–2 mm, longitudinally striate, sparsely puberulent around the pedicels, subtended by several broadly deltoid, ciliate bracteoles. Androecious flower in bud globose, 6–7 mm diam., ± glabrous, apiculate, the tepals fused, the pedicel 8–23 mm by 0.6–1 mm, glabrous or sparsely puberulent basally, subtended by a deltoid-subulate, ciliate bracteole 0.5–2.5 mm long; at anthesis deeply 4-fid, 20 mm diam., the lobes spreading flat; stamens numerous, ca. 200, lanceolate to subulate, 2.5–4 mm long by 0.7–1 mm wide, sessile or with a short filament, the loculi lateral, separate, occupying almost the entire length of the stamen, the connective slightly prolonged, obtusely apiculate, the internal receptacle surface glabrous. Gynoecious flower in bud subglobose, slightly depressed apically, 4–5 mm diam., externally glabrous to sparsely hirsutulous; at anthesis (?) 5–6 mm diam., the orifice circular, entire, 2–3 mm diam., comprising ca. ½ total width of the receptacle; styles numerous, several hundred, shortly columnar, 0.2–0.3 mm long, the apex rounded, the internal receptacle surface puberulent around the orifice and be-

tween the styles, the pedicel 6–8 mm long, shorter than in the androecious flower. Mature fruiting receptacle cupuliform, attaining 150 mm diam. (fide notes on *Anon. sub SF 2126*, MAD); carpels unknown.

Distribution. Endemic to Madagascar (Fig. 30).

Habitat. The type of *Tambourissa madagascariensis* was collected on the Tsaratanana massif (northern Madagascar), presumably in montane wet forest of *Tambourissa/Weinmannia* above 1,000 m. The three other known collections of this species are from montane *Tambourissa/Weinmannia* wet forest (800–1,000 m), and Myristicaceae/*Anthostema* wet forest (ca. 400–800 m) in the eastern region. This seemingly disjunct distribution pattern may be the result of undercollecting.

MADAGASCAR. TAMATAVE: Mt. Ambatosoratra, 400 m, 4 Jan. 1949 (fl), *Anon. sub Herb. Alaotra 3247* (MAD); forest N of the road to Nickelville, on the banks of the Amkotreano River, 29 Dec. 1944 (fr), *Anon. sub Herb. Alaotra 2126* (MAD); wooded area on the summit of Mt. Analavorikely, 29 Dec. 1944 (fr), *Anon. sub Herb. Alaotra 2142* (MAD).

Tambourissa madagascariensis is anomalous in a number of respects and does not readily fit into any of the more or less natural groups of Madagascan species, but is best placed in species Group 2A. Its small, thin glabrous leaves are reminiscent of *T. purpurea* and *T. gracilis*, but the flowers are borne in long, slender subglabrous and long-pedicelled pleiochasia that are more suggestive of *T. gracilis*, *T. beanjadensis*, and *T. parvifolia*. Androecious flowers of *T. madagascariensis* are relatively large, however, and split open into four lobes which spread flat and bear numerous (ca. 200) long stamens with separate, parallel loculi, thus differing strikingly from the small, globular, nearly closed androecious flowers of *T. gracilis* and *T. purpurea*, which have short, sessile stamens with apically confluent loculi.

Gynoecious flowers of *Tambourissa madagascariensis* are small and globose-depressed with an entire, circular orifice that is internally puberulent, and numerous short, columnar-rounded styles suggestive of those species which produce copious mucilage at anthesis. The orifice apparently remains open throughout much of the floral development, thus differing markedly from the gynoecious flowers of *T. beanjadensis* and *T. parvifolia* (unknown in *T. gracilis*), which open by an X-shaped orifice at anthesis and, furthermore have conical styles.

In terms of both androecious and gynoecious floral structure, *Tambourissa madagascariensis* appears to be most closely related to two of the Comorean species in Group 2A, *T. comorensis* and *T. leptophylla*, although their leaves and flowers are much larger. Presence of abundant oil cells in the gynoecious floral ground tissue of all three species and large fruits are common features. This group of Comorean species could have been derived from a common ancestor similar to *T. madagascariensis*.

Tambourissa madagascariensis also appears to share characters of androecious and gynoecious floral morphology with *T. elliptica* subsp. *micrantha* from Réunion, notably the pleiochasial inflorescence, similar androecious flowers and stamens, and gynoecious flowers with short, columnar styles and a mucilaginous exudate. Gynoecious flowers of the latter species lack the open, circular orifice, however.

Vernacular names. Ambora, Mahimasina, Valiramarnia (Madagascar).

13. Tambourissa elliptica (Tul.) A.DC., Prodr. 16(2): 660. 1868; Cordem., Fl. Réunion 301. 1895; Perk. & Gilg, Pflanzenr. 4, 101: 71. 1901. *Ambora elliptica* Tul., Ann. Sci. Nat. (Paris) 4(3): 31. 1855; Tul., Monogr. Monim. 304. 1855. TYPE: Réunion. Woods of the Hauts de la Rivière des Galets, July 1851 (fr), *Boivin s.n.* (holotype, P).

Tambourissa amplifolia sensu Cordem., Fl. Réunion 301. 1895 non (Boj. ex Tul.) A.DC.

Treelet or tree of variable habit, attaining 12 m tall, the new growth glabrous or with sparse, scattered hairs, the mature leafy stems terete, 2–6(–8) mm diam. Leaves glabrous, opposite to subopposite, petiolate; petioles (8–)10–25 mm by 1.5–5 mm; lamina chartaceous to coriaceous, narrowly to broadly elliptic, oblong, obovate-elliptic, obovate, broadly obovate or orbiculate, (50–)80–180(–250) mm by (15–)25–140(–190) mm, the apex shortly acuminate, acute, obtuse or rarely rounded, the base acutely decurrent, acutely cuneate to obtuse, truncate or subcordate, the secondary veins (5–)6–12 pairs, making a 55–75° angle with the costa, the venation prominent, raised, visible to 3–4(–5°) adaxially, to 4–5(–6°) abaxially, the margin plane to slightly revolute. Leaves of seedlings and suckers hetero-

phyllous, small and apically dentate in subsp. *elliptica,* long, narrow and entire in subsp. *micrantha.* Inflorescence subglabrous, a short ramiflorous pleiochasium (in subsp. *micrantha*), or the flowers solitary, sometimes axillary (in both subspecies), or cauliflorous and the flowers solitary or in fascicles of 2–3 (in subsp. *elliptica*). Androecious flower in bud globose, 7–15 mm diam., apiculate with 4 minute, obtuse tepals, the pedicel 10–40(–60) mm by 1–1.5 mm; at anthesis (3–)4(–5)-fid, 16–45 mm diam., the lobes spreading flat; stamens numerous, 65–300, ligulate to linear-ellipsoid, 1.5–6.5 mm long by 0.5–1 mm wide, the filament distinct, the loculi lateral, comprising ⅔–¾ total length of the stamen, separate or confluent at the obtuse apex, the connective not prolonged, the internal receptacle surface glabrous. Gynoecious flower in bud globose-depressed to napiform-depressed, apiculate with several pairs of minute tepals, the pedicel (5–)10–20(–40) mm by 0.6–2 mm; at anthesis 6–15 mm diam., the orifice X-shaped, 1–5 mm wide, splitting into 4 shallowly deltoid lobes; styles numerous, ca. 150–200 or more, bluntly columnar, polyhedral, 0. 5 mm long by 0.2–0.5 mm wide, the internal receptacle surface glabrous or with rare scattered hairs, producing a mucilaginous exudate. Fruiting receptacle solitary or in clusters of 2–3 on the trunk (subsp. *elliptica*), or on the leafless branches (subsp. *micrantha*), urceolate-globose or cupuliform, 25–90 mm diam. by 15–50 mm long, the orifice subentire, comprising ca. ⅕–½ total width of the fruit, the external surface pale corky brown or mottled with dark patches, the internal surface subglabrous with short scattered, columnar-polyhedral styles 0.5 mm wide. Mature carpels ovoid, 9–12 mm long, 5–7 mm wide, 3–4 mm thick, the endocarp whitish (subsp. *elliptica*) or pale brown (subsp. *micrantha*).

Distribution. Endemic to the wet and cloud forest zones of Réunion Island (Fig. 31).

E. J. de Cordemoy recognized four species of *Tambourissa* in his "Flore de l'Ile de la Réunion" (1895), but used names of a Madagascan (*T. religiosa*) and a Mauritian (*T. quadrifida*) species for two endemic Réunion taxa that I have named *T. crassa* and *T. elliptica* subsp. *micrantha* respectively (Lorence, 1982).

Tambourissa elliptica, the only previously described species from Réunion, is quite polymorphic, but two modally distinct subspecies are distinguishable both by morphology, and, to a lesser degree, altitudinal distribution. Both subspecies are monoecious with pink or pale yellowish white flower color morphs (never dark purple as is *T. crassa*), caulinary flowers, conspicuous higher order venation, contain stone cells in the floral ground tissue, and have a less well-developed hypodermis than in *T. crassa,* the second Réunion species.

Subspecies *elliptica* consists of a series of mostly mid to upper elevation forms which Cordemoy considered to represent two distinct species (*T. elliptica* and *T. amplifolia,* respectively), based on leaf characters which prove to be variable. Subspecies *micrantha* usually occurs at lower elevations, particularly in the southeastern part of the island where the most lowland wet forest still remains.

Each subspecies tends to occupy its own altitudinal zone throughout much of Réunion (Fig. 31), at least in higher altitude wet and cloud forest, significant portions of which are still preserved due to the island's accentuated relief and steep, inaccessible slopes largely unsuitable for cultivation. A thorough distributional analysis is not possible for the lowlands, however, because little natural wet forest habitat remains there.

KEY TO THE SUBSPECIES OF *TAMBOURISSA ELLIPTICA*

1a. Flowers large, usually solitary or fasciculate, cauliflorous or ramiflorous; androecious buds 13–14 mm diam.; expanded androecious flowers 30–45 mm diam., the stamens ca. (100–)200–300 in number, (3–)4–6.5 mm long; gynoecious flowers 10–12 mm diam.; fruiting receptacle 45–90 mm diam.; sparse treelets or small, slender trees; medium to high elevations (1,000–2,000 m, rarely lower) ..... 13a. subsp. *elliptica*

1b. Flowers smaller, usually in pleiochasia, sometimes solitary, always ramiflorous or axillary; androecious buds 8–10 mm diam.; expanded androecious flowers 20–25(–27) mm diam.; large trees with dense crowns; lower elevations, (200–600 m, rarely higher) ..... 13b. subsp. *micrantha*

13a. Tambourissa elliptica subsp. **elliptica.**

Monoecious or subdioecious treelet or small tree attaining 6 m tall and 25 cm D.B.H., the bark soft, corky, pale brown, the new growth glabrous, rarely with a few scattered hairs, the mature leafy stems terete, 3–6(–8) mm diam. Leaves glabrous, opposite to subopposite, petiolate; petioles 10–25 mm by 2–5 mm; lamina subcoriaceous to coriaceous, elliptic to broadly

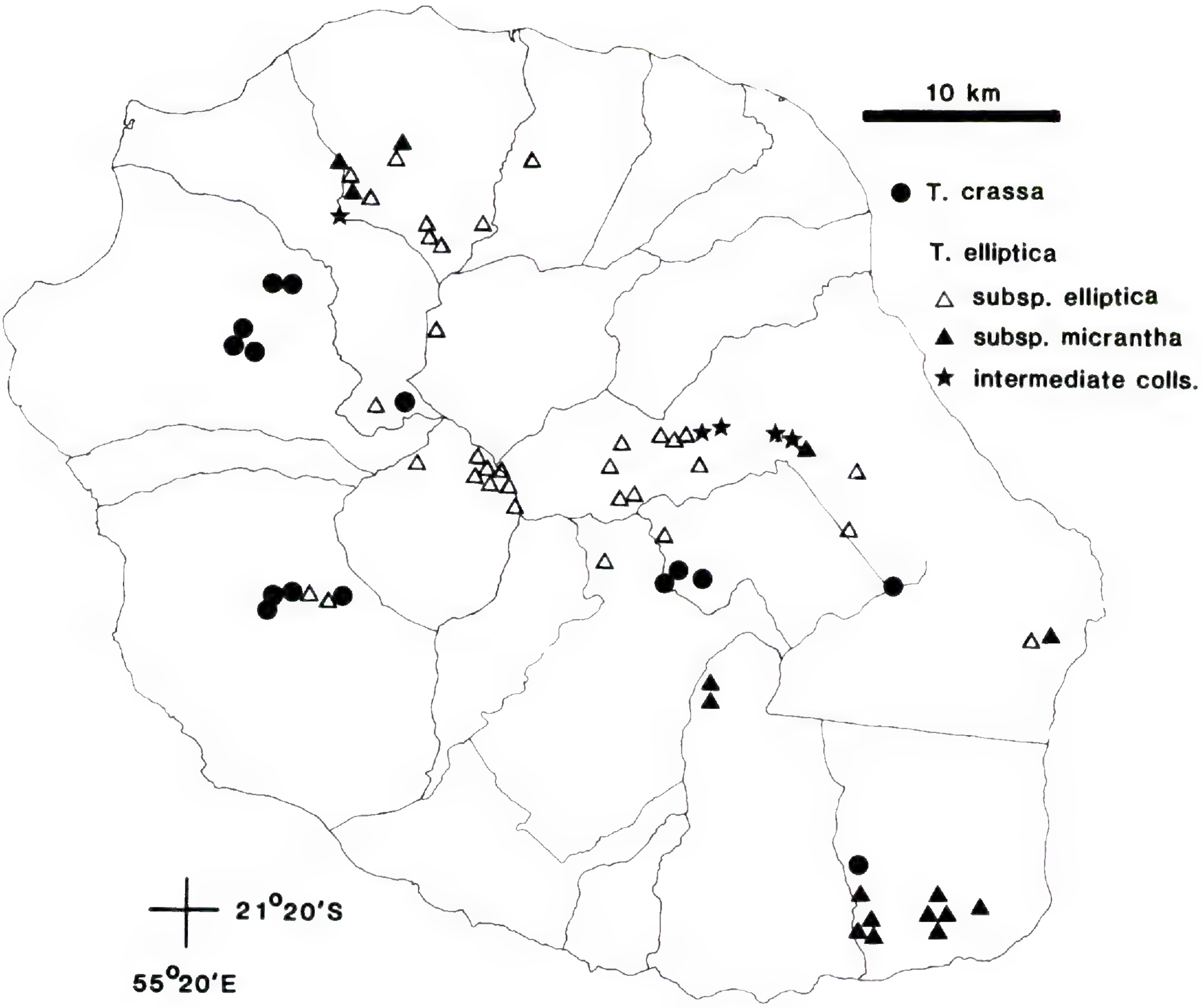


FIGURE 31. Distribution map of *Tambourissa* in Réunion.

elliptic, obovate to broadly obovate or orbiculate, 100–180(–250) mm by 60–140(–190) mm, the apex acute, rarely acuminate, obtuse or retuse, the base acute to obtuse, cuneate to decurrent, truncate or subcordate, the secondary veins 6–8 pairs, making a 55–75° angle with the costa, the venation prominent, visible to 3(–4°) adaxially and to 4(–5°) abaxially, the margin slightly revolute; juvenile and sucker leaves heterophyllous, with 1–2 pairs of glandular teeth in the apical portion of the lamina, the petiole red when living. Inflorescence glabrous or rarely with scattered hairs, the flowers solitary or in fascicles of 2–3 on meristematic swellings along the trunk, or the flowers ramiflorous and usually solitary, either axillary or on leafless nodes. Androecious flower in bud globose, (8–)12–15 mm diam., apiculate with several ± coalescent pairs of minute, glabrous tepals, the pedicel 20–40(–60) mm by 1–1.5 mm, jointed near the base with the short peduncle, subtended by several pairs of small, deltoid, decussate ciliate bracteoles; at anthesis 4(–5)-fid, 30–45 mm diam., the lobes spreading flat; stamens numerous, (100–)200–300, ellipsoid to linear, 3–5 mm long by 0.6–1 mm wide, the filament broad, distinct, comprising ca. ¼–⅓ total length of the stamen, the loculi subparallel, lateral, connivent or confluent at the obtuse apex, comprising ⅔–¾ total length of the stamen, the connective not prolonged, the internal receptacle surface glabrous, glaucous. Gynoecious flower in bud globose-depressed to napiform-depressed, apiculate with several pairs of minute, ± coalescent tepals, the pedicel 5–10(–40) mm by 1.2–2 mm, jointed near the base with the short peduncle, subtended by several pairs of decussate bracteoles; at anthesis 8–15 mm diam. by 5–10 mm long, the orifice 4-fid, 2–5 mm diam., X-shaped with 4 short, straight to incurved deltoid lobes; styles numerous, ca. 200 or more, bluntly columnar, ca. 0.5 mm long by 0.2–0.5 mm wide, ± polyhedral, the internal receptacle

surface glabrous or with rare, scattered hairs. Fruiting receptacle solitary on the trunk or major branches, urceolate-globose, 45–90 mm diam. by 30–50 mm long, the orifice 10–30 mm diam., comprising ⅕–⅓ total width of the receptacle, subentire with remnants of the lobes, the external surface light corky brown, the internal surface glabrous, corky, with numerous short, ± polyhedral styles ca. 0.5–1 mm wide by 0.2–0.5 mm long, the apex flat or depressed, the pedicel and peduncle 10–60 mm long by 8–10 mm diam. Mature carpels ovoid-compressed, 10–12 mm long, 5–6 mm wide, 3–4 mm thick, the endocarp whitish, the surface smooth, unsculptured. Gametic chromosome number $n = 19$.

Distribution. Endemic to Réunion (Fig. 31).

Habitat. It ranges from lower montane wet forest at altitudes from ca. 200 to 1,100 m, to cloud forest at altitudes from ca. 1,100 to 2,000 m.

RÉUNION. BÉBOUR: from Bébour to Casse de Tacamaca, 1,350–1,220 m, 18 Jan. 1975 (fl), *Bernardi 15151* (G, 2 sheets; P); Bébour Plateau, 8 Nov. 1972 (fr), *Bosser 21498* (P); on Piton Rond, ca. 1,800 m (fl), *Coode et al. 4223* (K, REU); Piton Rond, 1,300–1,600 m, 23 Feb. 1979 (fl), *Lorence 2431* (MAU, MO); (fl), *Lorence 2432* (MO); (fl, fr), *Lorence 2433* (MAU, MO). BOIS BLANC: Hauts de Bois Blanc, 600 m, July 1972 (fr), *Friedmann 1891* (P). BRAS JEANNE: Oct. 1944 (st), *Rivals s.n.* (TL-R); along canal of Bras Jeanne, Oct. 1944 (st), *Rivals s.n.* (TL-R). BRÛLÉ DE ST. DENIS: Hauts du Brûlé de St. Denis, Mar. 1943 (st), *Rivals s.n.* (TL-R); Ilet à Quinquina, near St. Denis, July 1945 (st), *Rivals s.n.* (TL-R). CIRQUE DE CILAOS: Mare à Joseph forest, 1,400 m, 25 Mar. 1967 (st), *Cadet 664 bis* (REU); 19 July 1975 (fl), *Cadet 4946* (REU); 22 Feb. 1975 (fl), *Cadet 5062* (REU); Petit Matarum, 1,700 m, 22 Feb. 1975 (fl), *Cadet 5055* (REU); R bank of Bras de Benjoin, road to Cilaos, 950 m, 3 Feb. 1968 (fl), *Capuron 28002-SF* (P, 2 sheets); Mare à Joseph above Cilaos, 1,400 m, 23 Feb. 1975 (fr), *Coode 4928* (K); (fl), *Coode 4929* (K); Coteau Kerveguen cloud forest, 1,500–1,700 m, 24 Feb. 1979 (st), *Lorence & Rolland 2437* (MAU, MO); (fl), *Lorence & Rolland 2438* (MO); (fl, fr), *Lorence & Rolland 2439* (MAU, MO); (fl), *Lorence & Rolland 2440* (MAU, MO); (fl), *Lorence & Rolland 2441* (MAU, MO); (fl, fr), *Lorence & Rolland 2442* (MAU, MO); Grand Matarum and Mare à Joseph, Aug. 1943 (st), *Rivals s.n.* (TL-R); Ilet des Salazes, Cilaos, 1,300 m, 21 Feb. 1944 (fl), *Rivals s.n.* (TL-R); slopes of the Piton des Neiges, 1,900–2,000 m (fr), *Rivals s.n.* (TL-R); Mare à Joseph, 1,200 m (fr), *Rivals s.n.* (TL-R). CIRQUE DE MAFATE: Mafate, Aug. 1883 (st), *Cordemoy s.n.* (TL-R); Sentier des Scouts, from Le Belier to top of Galets Gorge, ca. 1,800 m (fl), *Richardson 4136* (K). MOKA: Moka (st), *Rivals s.n.* (TL-R); 20 Feb. 1945 (fl), *Rivals s.n.* (TL-R); Hauts de Moka at the Chabries, 600 m, Apr. 1946 (fr), *Rivals s.n.* (TL-R). LA MONTAGNE: Grande Montagne, 1,200 m, 22 Mar. 1968 (fr), *Cadet 1291* (REU). NOUVELLE: La Nouvelle, near forestry station, May 1949 (fl), *Rivals s.n.* (TL-R). PITON RAVINE À MALHEUR: heights of Piton de la Ravine à Malheur, 900 m, May 1943 (st), *Rivals s.n.* (TL-R). PLAINE D'AFFOUCHES: forest along path to Plaine d'Affouches, 900 m, May 1943 (st), *Rivals s.n.* (TL-R). ROCHE ECRITE: path to Roche Ecrite, 28 Feb. 1975 (fl), *Coode 5000* (K, 2 sheets; REU); 5 Oct. 1938 (st), *Rivals s.n.* (TL-R). PLAINE DES CAFRES: Plaine des Cafres (st), *Cordemoy s.n.* (TL-R); Piton Bleu, 26 Sept. 1882 (st), *Cordemoy s.n.* (TL-R). PLAINE DES CHICOTS: near Mamode Camp, 1,200 m, 27 Dec. 1966 (st), *Cadet 595* (REU). PLAINE DES MAKES: Domainial line above Tévelave, along edge of Plaine des Makes, Oct. 1943 (st), *Rivals s.n.* (TL-R); ravine of the Col à Maison Rouge, 28 June 1967 (st), *Cadet 1039* (REU). PLAINE DES MERLES: Salazie, 1,200 m, 19 Feb. 1944 (fl), *Rivals s.n.* (TL-R). PLAINE DES PALMISTES: Petite Plaine above Plaine des Palmistes, cloud forest, 1,200 m, 25 Feb. 1979 (fl), *Lorence & Rolland 2454* (MO); 13 Jan. 1973 (fl, fr), *Cadet 4021* (REU). SAINTE ANNE: above Sainte Anne, 1,200 m, 30 May 1974 (fr), *Cadet 4714* (REU); near Sainte Anne bridge (st), *Cordemoy s.n.* (TL-R). TAKAMAKA: Takamaka forest, Ilet à Bananes, 600–1,000 m, 10 Mar. 1979 (fl), *Lorence & Rolland 2525* (MAU, MO); (fl), *Lorence & Rolland 2526* (MO); (fl), *Lorence & Rolland 2527* (MAU, MO); (fl, fr), *Lorence & Rolland 2528* (MAU, MO); (fl), *Lorence & Rolland 2529* (MO); (fl, fr), *Lorence & Rolland 2530* (MAU, MO); path to Bras Cabot, slopes of the Ilet de Patience, 1,200–1,500 m, Feb. 1971 (fl), *Bosser 20578* (P); Grand Fond forest, Takamaka, 900 m, 23 July 1943 (st), *Rivals s.n.* (TL-R). WITHOUT PRECISE LOCALITY: 1836–1837 (fl), *Gaudichaud s.n.* (P); (st), *Rivals s.n.* (TL-R).

Both the upland and lowland forms of *Tambourissa elliptica* subsp. *elliptica* include individuals with either pink or pale greenish to yellowish white floral color morphs (as does subsp. *micrantha*), but never dark purple as in *T. crassa*. Floral odors of both *T. elliptica* subsp. *elliptica* and *T. crassa* are strong and rancid-fruity with overtones of butyric acid, never pleasantly sweet-fruity as in subsp. *micrantha*. In addition, gynoecious flowers of both subspecies of *T. elliptica* and also of *T. crassa* are morphologically similar and produce a mucilaginous exudate that partly fills the floral cup. Strong similarities in the floral construction of all three Réunion taxa suggest a fairly recent derivation from a single, common ancestor. Both species belong to Group 2A.

Although upland and lowland forms of *Tambourissa elliptica* subsp. *elliptica* are quite distinct in their extremes, they intergrade gradually and clinally. For example, collections from Takamaka (eastern Réunion) form a continuous series ranging from lowland wet forest at 600–700 m elevation, to the lower limits of cloud forest at 900–1,000 m (*Lorence & Rolland 2525–2530*, all MO). Both forms are diploids with $n = 19$. Because they are not separable by any single con-

stant character, nor even by any constant constellation of characters, it is not possible to recognize them formally as taxa. The type of subsp. *elliptica* from the Hauts de la Rivière des Galets (*Boivin s.n.,* P) represents an intermediate form, although most closely approaches the upland type.

Vernacular names. Bois de bombarde, Bois de bombarde à grandes feuilles (Réunion).

13b. Tambourissa elliptica subsp. **micrantha** Lorence, Bull. Mus. Hist. Nat. (Paris), Ser. 4, Sect. B, Adansonia 3(3): 298, pl. 2, fig. 8. 1982. TYPE: Réunion. Brûlé de Baril: lower montane wet forest, ca. 300 m, 2 Mar. 1979 (fl), *Lorence, Lorence & Cadet 2489* (holotype, MO; isotypes, K, MAU, P, REU, Z).

T. quadrifida sensu Cordem., Fl. Réunion 301. 1895 non Sonn.

Monoecious canopy tree 10–12 m tall and 30 cm D.B.H., the bark soft, pale yellow-brown, corky and peeling, the new growth with sparse, short simple hairs, soon glabrous, the mature leafy stems 2–5 mm diam. (to 8 mm diam. on suckers), longitudinally striate. Leaves glabrous, opposite to subopposite, petiolate; petioles (8–)10–20 mm by 1.5–2 mm; lamina chartaceous to subcoriaceous, elliptic, narrowly elliptic, oblong or obovate-elliptic, (50–)80–180(–220) mm by (15–)25–50(–65) mm, the apex shortly acuminate, shortly acute, obtuse or rarely rounded, the base acutely cuneate to acutely decurrent, the secondary veins (5–)7–12 pairs, making a 55–65° angle with the costa, the venation prominent, finely reticulate, visible to 4(–5°) adaxially and to 5(–6°) abaxially, the margin plane to slightly revolute; juvenile and sucker leaves heterophyllous, long and narrowly elliptic, the lamina attaining 180 mm by 40 mm, the apex acute to acuminate, the secondary veins 10–14 pairs, the petiole and costa bright red when living. Inflorescence ramiflorous on old or new stems, or axillary, a unisexual or sexually mixed pleiochasium of 3–7 flowers, with sparse scattered hairs, the floral axis 8–20 mm by 1–1.5 mm, subtended by several minute, ciliate naviculate bracteoles 0.6–0.8 mm long, or the flowers rarely solitary. Androecious flower in bud globose to globose-depressed, 7–9 mm diam., the apex with 4 minute, obtuse tepals, the pedicel 10–28 mm by 1 mm, subtended by a minute bracteole; at anthesis (3–)4-fid, 16–26 mm diam., the lobes spreading flat; stamens 65–95, ligulate, 1.5–2.5 mm long, 0.5–0.8 mm wide, the filament short, the loculi lateral, comprising ca. ⅔–¾ total length of the stamen, apically connivent or confluent, the connective not prolonged. Gynoecious flower in bud napiform-depressed, apiculate with 4 minute tepals, the pedicel (5–)10–20 mm by 0.6–0.8 mm, subtended by a single bracteole; at anthesis 6–7 mm diam. by 4–6 mm long, the orifice X-shaped, 1–2 mm diam., splitting into 4 suberect deltoid lobes; styles numerous, ca. 150–160, short, bluntly columnar, 0.5 mm long by 0.3–0.4 mm wide, interspersed with rare, scattered hairs. Fruiting receptacle solitary or in clusters of 2–3 on leafless branches, cupuliform-urceolate, 25–45 mm diam. by 15–30 mm long, the orifice 6–14 mm diam., comprising ca. ⅓–½ total width of the fruit, subentire, the walls 10–15 mm thick, the external surface dark reddish brown mottled with pale corky patches, the internal surface with scattered, short, bluntly columnar-polyhedral styles ca. 0.3–0.5 mm long by 0.5 mm wide, interspersed with rare, scattered hairs, the pedicel and peduncle 12–16 mm by 3–6 mm. Mature carpels 9–11 mm long, 5–7 mm wide, 3–4 mm thick, the endocarp pale brown, the surface with rugose striations. Gametic chromosome number: $n = 19$. Figure 32.

Distribution. Endemic to Réunion (Fig. 31).

Habitat. Tambourissa elliptica subsp. *micrantha* is occasional to locally common from ca. 300 to 700 m in the southern sector of Réunion on the lower slopes of the active volcano, the Piton de la Fournaise (le Volcan) massif (at Basse Vallée, Brûlé de Baril, Forêt de la Mare Longue, Mare d'Arzul, and Bois Blanc). Collections are also known from l'Echo below Plaine des Palmistes (ca. 700 m), and the subspecies reaches ca. 1,000 m at Brûlé de St. Denis and Plaine d'Affouches.

RÉUNION. BOIS BLANC: 300 m, Apr. 1949 (fl), *Rivals s.n.* (TL-R). BRÛLÉ DE ST. DENIS: rainy season (Dec.–Feb.) 1945 (fr), *Rivals s.n.* (TL-R). BASSE VALLÉE: Béloni, 21 Oct. 1971 (fr), *Friedmann 3265* (P). BRÛLÉ DE BARIL: 26 Feb. 1975 (fl), *Coode et al. 4963* (K, 2 sheets; REU); 300 m, 2 Mar. 1979 (st), *Lorence, Lorence & Cadet 2487* (MAU, MO); (fl), *Lorence, Lorence & Cadet 2488* (B, K, MAU, MO, P, REU, Z); 13 July 1979 (fr), *Lorence & Cadet 2741* (MO); (fr), *Lorence & Cadet 2742* (MAU, MO); (fr), *Lorence & Cadet 2743* (B, K, MAU, MO, P, REU, Z). DOS D'ANE: 1,200 m, Mar. 1974 (fl), *Friedmann 2299* (P, intermediate form). GRAND ÉTANG: (E Réunion) ca. 500 m, 15 July 1979 (fl), *Lorence & Rolland 2758* (MO, intermediate form). L'ECHO: St. Benôit to Plaine des Palmistes route, 700 m, 4 July 1967 (st), *Cadet 1038 bis* (REU); (st), *Cadet*

FIGURE 32. *Tambourissa elliptica* (Tul.) A.DC. subsp. *micrantha* Lorence.—A. Habit.—B. Androecious flower at anthesis, apical view.—C. Androecious flower at anthesis, lateral view.—D. Stamen, abaxial view.—E. Stamen, adaxial view.—F. Gynoecious flower at anthesis, apical view.—G. Gynoecious flower at anthesis, longitudinal section.—H. Submature fruiting receptacles. A–G. *Lorence 2489* (MO). H. *Lorence 2741* (MO). Bars equal 10 mm in A–C, F–H, and 1 mm in D, E.

1039 bis (REU, intermediate form); 27 Feb. 1979 (st), *Lorence 2462* (MO, intermediate form). PLAINE D'AFFOUCHES: La Montagne, road to Plaine d'Affouches, 1,000 m, pk 4.5, 27 Dec. 1966 (st), *Cadet 612* (REU); (fr), *Rivals s.n.* (TL-R). RIVIÈRE DES REMPARTS: high valley of the Rivière des Remparts, 1,000 m, 7 Mar. 1975 (fl), *Cadet 5123* (REU, intermediate form); 1,100 m, (fl), *Cadet 5124* (REU, intermediate form). ST. PHIL-

IPPE: Mare d'Arzul forest, 9 Dec. 1943 (st), *Rivals s.n.* (TL-R); St. Philippe (st), *Rivals s.n.* (TL-R); Mare Longue forest, 400–780 m, 14–15 Jan. 1975 (fr), *Bernardi 15044* (G, 3 sheets; P, REU); ca. 500 m, 25 Feb. 1975 (fl), *Coode et al. 4956* (K, 2 sheets; REU); 250–500 m, 2 Mar. 1979 (fl), *Lorence, Lorence & Cadet 2483* (MAU, MO); Jan. 1949 (st), *Rivals s.n.* (TL-R); May 1943 (st), *Rivals s.n.* (TL-R). TAKAMAKA: Takamaka forest, Ilet à Bananes, ca. 800–900 m, 10 Mar. 1979 (fl), *Lorence & Rolland 2524* (MO, intermediate form). WITHOUT PRECISE LOCALITY: 1853–1863 (fl, fr), *Frappier 4* (P, 5 sheets).

At Brûlé de Baril, *Tambourissa elliptica* subsp. *micrantha* becomes a subcanopy or canopy tree attaining 10–12 m with a straight trunk attaining 25–30 cm D.B.H. and a narrow, compact crown with numerous, erect branches. It differs most conspicuously from subsp. *elliptica* in having elliptic to narrowly elliptic leaves with a laminar length to width ratio exceeding 2:1 and often approaching 3:1. Juvenile and sucker leaves of subsp. *micrantha* are longer and narrower than its adult leaves, have more numerous secondary veins, bright red petioles and midribs when living, but lack dentate margins. Subspecies *elliptica* has instead apically dentate-serrate juvenile leaves, as do most other congeners for which data is available.

Flowers of both sexes are conspicuously smaller than in subsp. *elliptica,* hence the epithet *micrantha.* Large individuals of subsp. *micrantha* are monoecious, often with sexually mixed pleiochasia, whereas sex expression appears to be size and/or age related in subsp. *elliptica.* Flowers of subsp. *micrantha* are generally pleiochasial and ramiflorous or axillary, whereas those of subsp. *elliptica* tend to be cauliflorous, sometimes axillary. Fruits of subsp. *micrantha* are generally smaller, often produced in clusters of two or three on the branches, and are more conspicuously mottled in contrast to the larger, solitary and often caulinary fruits of subsp. *elliptica* which are more uniformly pale brown.

Although the two subspecies of *Tambourissa elliptica* occur together in certain areas of wet forest at low to medium altitudes (e.g., Hauts du Bois Blanc; Hauts du Brûlé de St. Denis) and remain distinct there, they intergrade in other localities, e.g., Takamaka (*Lorence & Rolland 2524,* MO), Dos d'Ane (*Friedmann 2299,* P), Rivière des Remparts (*Cadet 5123, 5124,* REU), and Grand Etang (*Lorence & Rolland 2758,* MO). Both subspecies have $n = 19$. Despite occasional intermediate collections, the two taxa are separable by relatively constant, modally distinct characters of floral size and odor, staminal length and number, ratio of laminar length to width, and fruit size. I have therefore chosen to recognize them as subspecies.

Tambourissa elliptica subsp. *micrantha* belongs to species Group 2A. In view of its monoecy, less reduced pleiochasial inflorescences, and flowers intermediate in size and number of parts, it seems to be the least specialized of the Réunion taxa and therefore probably most like the ancestral species from which the others were derived.

Vernacular names. Bois de bombarde, Bois de bombarde à petites feuilles (Réunion).

14. Tambourissa crassa Lorence, Bull. Mus. Hist. Nat. (Paris), Ser. 4, Sect. B, Adansonia 3(3): 298, pl. 2, fig. 7. 1982. TYPE: Réunion. Road to Maïdo above Petite France, on forestry road C.F. 81; low cloud forest, ca. 1,200–1,400 m, 19 July 1979 (fl), *Lorence 2780* (holotype, MO; isotypes, K, MAU, P, REU, Z).

T. religiosa sensu Cordem., Fl. Réunion 301. 1895 non (Tul.) A.DC.

Dioecious tree, rarely shrubby, 7–8 m tall, the trunk stout, to 30 cm D.B.H., the bark pale grayish brown, smooth to irregularly fissured-flaking, the crown compact, the new growth glabrous, rarely with a few scattered hairs, the mature leafy stems 4–9 mm diam., terete, glabrous, longitudinally wrinkled. Leaves glabrous, opposite to subopposite, petiolate to subsessile; petiole stout, 4–15(–20) mm by (2–)3–6 mm; lamina coriaceous, obovate, broadly obovate, broadly elliptic or suborbiculate, (40–)60–175 mm by (20–)40–140 mm, the apex obtuse, rounded, or retuse-emarginate, the base acutely cuneate to acutely decurrent, the secondary veins 5–6 pairs, making a 45–55° angle with the costa, the venation obscure, visible to 2(–3°) adaxially and to 3(–4°) abaxially, the margin moderately revolute, the color pale brown to bright yellow-green when dry. Inflorescence a solitary monochasium terminal on the leafy stems (the subtending leaves ± caducous), or rarely cauliflorous or ramiflorous and terminal on short, leafy or leafless bracteate shoots. Androecious flower in bud globose, 13–14 mm diam., glabrous, apiculate with 4 small, obtuse-deltoid, ± glabrous tepals, the pedicel and peduncle stout, erect or recurved, 15–32 mm by 4–5 mm, bearing several caducous,

ciliate deltoid bracteoles basally; at anthesis 4–5-fid, 32–45(–50) mm diam., the lobes thick, spreading almost flat or somewhat incurved, the internal receptacle surface glabrous; stamens numerous, ca. 125–250, ligulate-ellipsoid, 4–5 mm long by 1–1.5 mm wide, the filament short and thickened basally, the loculi lateral, comprising ca. ⅔–¾ total length of the stamen, usually confluent apically, occasionally free, the connective not prolonged. Gynoecious flower in bud napiform to globose-depressed, the apex with 4 small, obtuse or deltoid, glabrous or sparsely ciliate tepals, the pedicel and peduncle suberect, 8–25 mm by 2–4 mm, bearing several small, ± ciliate bracteoles basally; at anthesis urceolate-globose to urceolate-napiform, 12–14 mm diam. by 8–10 mm long, the walls thick, the apex splitting into 4(–8) thick, subequal, shallowly deltoid lobes, the orifice 5–6 mm diam., comprising ca. ¼–⅓ total width of the receptacle; styles numerous, ca. 200 or more, crowded, bluntly columnar, ca. 0.5 mm long by 0.3–0.5 mm wide, the internal receptacle surface glabrous, producing a mucilaginous exudate. Submature fruiting receptacle globose-urceolate, ca. 60 mm diam. by 40 mm long, corky brown externally, internally glabrous with numerous scattered, bluntly columnar polyhedral styles ca. 0.3 mm long by 0.5–0.8 mm wide, the pedicel and peduncle stout, ca. 50 mm by 10 mm. Mature carpels unknown. Figure 33.

Distribution. Endemic to Réunion (Fig. 31).

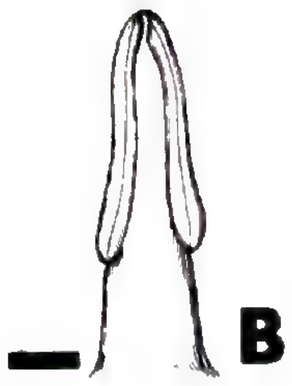
Habitat. *Tambourissa crassa* is local and occasional in cloud forest formations from ca. 1,200 to 2,000 m, rarely extending as low as 700 m (e.g., at Basse Vallée, *Bosser 21313*).

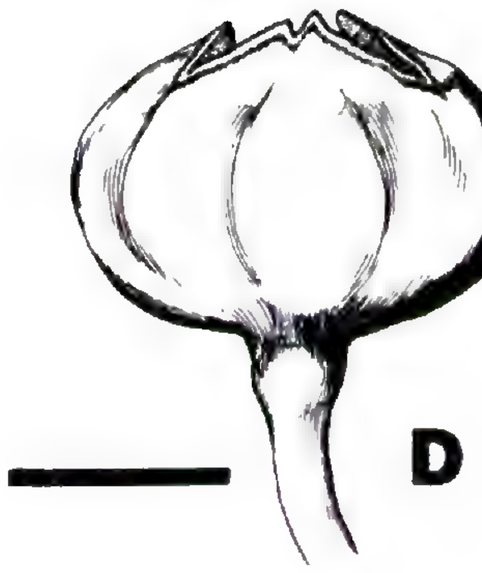
RÉUNION. BASSE VALLÉE: humid forest, 600–700 m, 20 Oct. 1972 (fr), *Bosser 21313* (P). BOIS DE NÈFLES: Hauts du Bois de Nèfles, St. Paul, 1,400 m, 17 Sept. 1979 (fl, fr), *Cadet 4790* (REU); (fl), *Cadet 4791* (REU). LES MARES: Les Mares, 1,500 m (fl), *Friedmann 3001* (P). MAÏDO: road to Maïdo above Petite France, 1,350 m, 22 Feb. 1979 (st), *Lorence & Cadet 2412* (MAU, MO); ca. 1,200 m, 22 Feb. 1979 (st), *Lorence & Cadet 2414* (MAU, MO). PLAINE DES CAFRES: (st), *Cordemoy s.n.* (TL-R); Col de Bellevue at Grande Montée de la Plaine des Cafres, low cloud forest, 1,600 m, 27 Feb. 1979 (fl), *Lorence 2468* (MAU, MO); (fl), *Lorence 2469* (MAU, MO); (fl), *Lorence 2470* (MO); 17 July 1979 (fl), *Lorence 2767* (K, MAU, MO, P, Z); summit of the slopes of the Grande Montée, 15 Mar. 1943 (st), *Rivals s.n.* (TL-R). PLAINE DES MAKES: 16 Mar. 1971 (st), *Friedmann 1031* (P). PLAINE DES PALMISTES: banks of the Ravine Petite à Bras des Calumets, 1,300 m, 17 Jan. 1972 (fl), *Cadet 3477* (REU). PLAINE DES SALAZES: 2,000 m, 19 Feb. 1944 (st), *Rivals s.n.* (TL-R). PLAINE DES TAMARINS: 1,800 m, below the Col de Fourche, Mafate, 28 Nov. 1974 (fl), *Cadet 4604* (REU). RIVIÈRE DE L'EST: low thicket along the Rivière de l'Est, 1,550 m, Nov. 1967 (fl), *Cadet 5717* (REU). TÉVELAVE: forestry road above Tévelave, cloud forest, 1,300–1,400 m, 28 Feb. 1979 (fl), *Lorence 2478* (MO); along the domainial line, 1,700 m, cloud forest transitional to heath formation, 6 Mar. 1979 (fl), *Lorence 2500* (MAU, MO); Hauts du Tévelave, 1,500–1,900 m (st), *Rivals s.n.* (TL-R). WITHOUT PRECISE LOCALITY: (st), *Rivals s.n.* (TL-R).

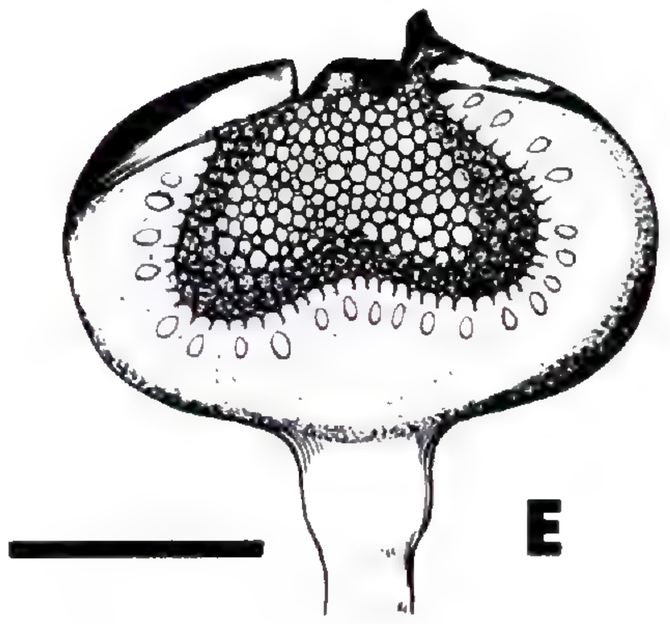
Tambourissa crassa belongs to species Group 2A and is most closely allied to *T. elliptica* subsp. *elliptica,* also from Réunion, from which it can be distinguished by its truly dioecious habit, thicker leaves, and solitary, terminal flowers and fruits borne at the ends of the top branches (rarely caulinary on short, leafy or leafless bracteate shoots, but even then solitary and terminal). The succulent, strongly discolorous leaves of *T. crassa* have a well-developed hypodermis 4–6 cell layers thick, which is only 2–3 cells thick in both subspecies of *T. elliptica.* Other distinguishing features are its somewhat pachycaulous habit, sparse and compact crown, the almost camphor-like fragrance of the dried specimens, and absence of stone cells and tanniferous idioblasts from the floral ground tissue.

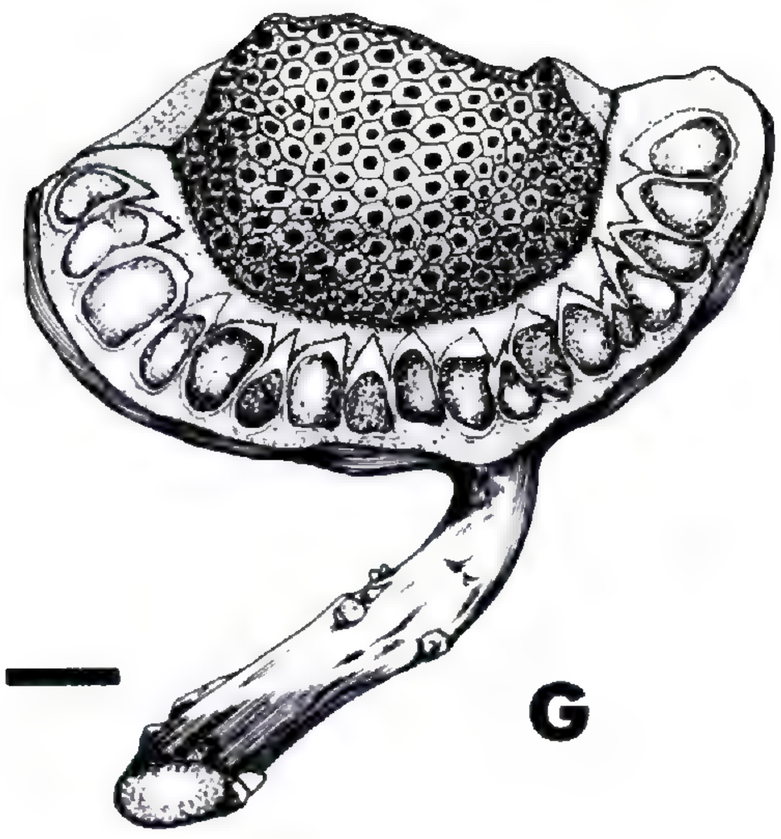
Unlike the more variable *Tambourissa elliptica* subsp. *elliptica, T. crassa* is quite stable morphologically. As in most species, a certain amount of intraspecific variation occurs in leaf size and shape, flower color, and number of stamens, but both species are quite distinct morphologically. Both *T. crassa* and *T. elliptica* subsp. *elliptica* frequently occur sympatrically in the cloud forest zone (1,200–2,000 m), e.g., at Hauts du Tévelave, and along the road to Maïdo, where neither intermediates nor putative hybrids were found. For these reasons I regard *T. crassa* as a discrete species rather than a subspecies of *T. elliptica* in spite of certain morphological similarities.

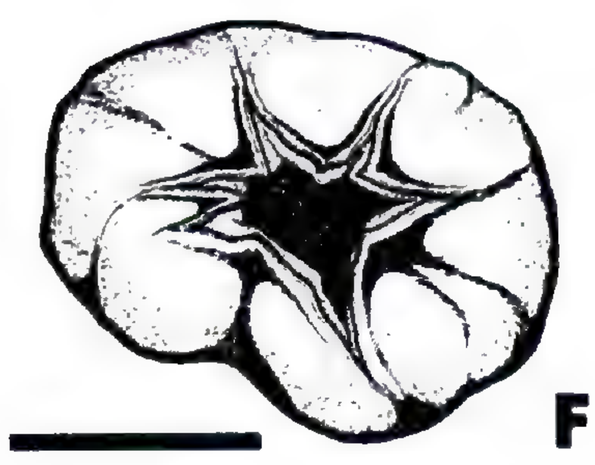
Both *Tambourissa crassa* and *T. elliptica* subsp. *elliptica* have large, structurally similar leaves and large flowers with numerous stamens and styles, which are presumably adaptations to a shared habitat and similar pollinators. Apparently both taxa have evolved from a common ancestor with less specialized features, which *T. elliptica* subsp. *micrantha* appears to approach most closely. *Tambourissa crassa* has attained the highest degree of specialization of the three Réunion taxa, however, in being dioecious and having inflorescences reduced to a single, terminal flower.











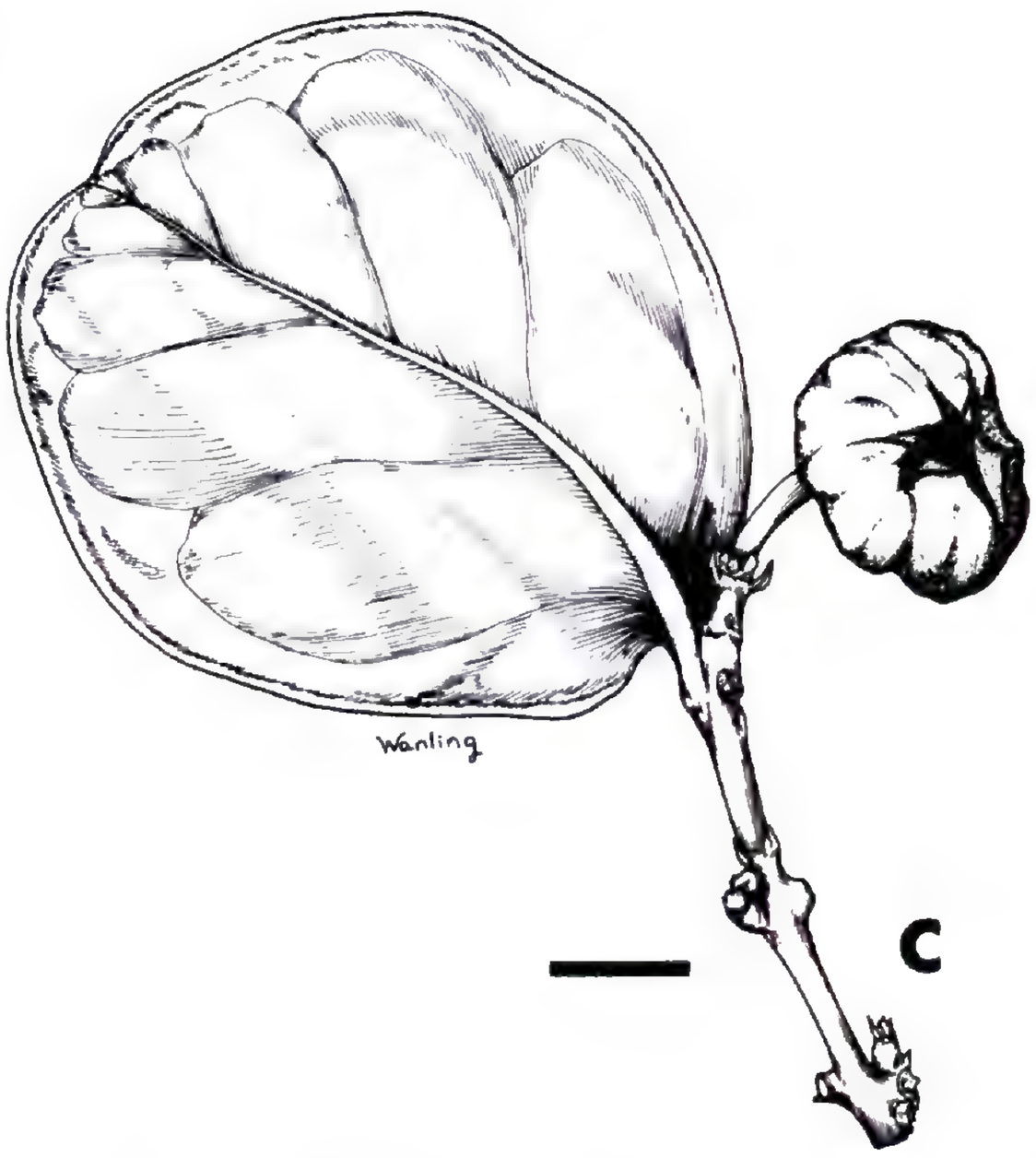


FIGURE 33. *Tambourissa crassa* Lorence.—A. Habit, with androecious flower at anthesis.—B. Stamen, adaxial view.—C. Habit, with gynoecious flower at anthesis.—D. Gynoecious flower at anthesis, lateral view.—E. Gynoecious flower at anthesis, longitudinal section.—F. Gynoecious flower at anthesis, apical view.—G. Fruiting receptacle, longitudinal section. A, B. *Lorence 2767* (MO). C–F. *Lorence 2780* (MO). G. *Cadet 4790* (REU). Bars equal 10 mm in A, C–G, and 1 mm in B.

Flowers of both sexes produce strong, rancid-fruity floral odors of butyric acid, as do those of *Tambourissa elliptica* subsp. *elliptica*. Both pale yellow-green and dark purple floral color morphs occur, although flower color appears to be constant within a given population (e.g., yellow at Col de Bellevue, purple at Hauts du Tévelave).

Vernacular names. Bois de bombarde, Bois de bombarde à grandes feuilles (Réunion).

15. Tambourissa comorensis Lorence, Bull. Mus. Hist. Nat. (Paris), Ser. 4, Sect. B, Adansonia 3(3): 295, pl. 1, figs. 3, 4. 1982. TYPE: Comore Archipelago. Grande Comore: La Grille forest above Maoueni, ca. 800 m, 29 July 1979 (fl, fr), *Lorence & Banfi 2878* (holotype, MO; isotypes, B, G, K, MAU, P, REU, Z).

Large monoecious canopy tree 15–20 m tall and 50 cm D.B.H., the bark pale brown, smooth, flaking, the new growth glabrous or with rare, scattered hairs, the mature leafy stems pale greenish, terete, glabrous, 3–4 mm diam. Leaves opposite to subopposite, glabrous, petiolate; petiole 10–28 mm by 1–1.5 mm; lamina chartaceous, elliptic, narrowly elliptic, ovate, oblong or lanceolate, (60–)80–140 mm by (20–)30–75 mm, the apex shortly acuminate, rarely acute or obtuse, the tip rounded, the base acutely cuneate to obtuse, generally slightly decurrent, the secondary veins 4–7 pairs, making a 50–60° angle with the costa, the venation prominent, visible to 4(–5°) on both surfaces, the margin plane to slightly revolute; juvenile leaves heterophyllous, the apical ½–⅔ of the lamina serrate-dentate with 1–5 pairs of large teeth, the petiole red when living. Inflorescence cauliflorous or ramiflorous, on meristematic swellings on the trunk or on leafless nodes of the branches, a short, unisexual or sexually mixed pleiochasium of 4–9 flowers, the floral axis 5–20(–60) mm by 2–3 mm, when young finely velutinous-pubescent with short, simple or fasciculate hairs, each pedicel subtended by a minute naviculate bracteole. Androecious flower in bud globose, 9–14 mm diam., externally puberulent to glabrous, ± pustular, apiculate with a small pore flanked by 2–4 pairs of dark, hirsutulous, broadly deltoid tepals, the pedicel 8–30 mm by 1–1.5 mm; at anthesis deeply 4(–6)-fid, 23–35 mm diam., the lobes spreading flat and reflexing slightly, the apex of each lobe with several fleshy tepals internally, the internal receptacle surface glabrous; stamens numerous, ca. 125–150, linear-ligulate, 2.5–4 mm long by 0.7–1 mm wide, the loculi separate, parallel, lateral or slightly abaxial, occupying almost the entire length of the stamen, the filament short, thick, the connective not prolonged. Gynoecious flowers 1–6 per inflorescence, terminal or lateral, the pedicel 12–20 mm by 2 mm; at anthesis broadly patelliform-urceolate, 12–15 mm diam. by 5–7 mm long, the orifice circular, entire, 7–10 mm diam., comprising ⅔ total width of the receptacle, the rim velutinous, open even in bud, the external surface puberulent, ± pustular; styles numerous, several hundred, coalescent, short, bluntly columnar-polyhedral, 0.3–0.5 mm long and wide, the apex papillose, the internal receptacle surface with scattered hairs. Fruiting receptacle solitary or in clusters of 2–3 on the trunk and major branches, irregularly cupuliform, often ± distorted, 90–175 mm diam. by 50–75 mm long, the orifice comprising ca. ⅓–½ total width of the receptacle, entire, subcircular, 45–90 mm diam., the walls 16–25 mm thick, externally smooth, mottled reddish brown, internally glabrous with numerous scattered columnar-polyhedral styles 0.3–0.4 mm long by 0.5–0.8 mm wide. Mature carpels ovoid to ellipsoid, compressed, 11–13 mm long, 5–8 mm wide, 4–6 mm thick, the endocarp dark brown to black, the surface scrobiculate. Gametic chromosome number, $n = 19$. Figure 34.

Distribution. Endemic to Grande Comore (Fig. 35).

Habitat. *Tambourissa comorensis* occurs in lower montane wet forest formations. All known collections are from La Grille forest above Maoueni (northern part of the central ridge, 800–900 m), and from forest above Ntsorale Dimane along the eastern part of the same massif (250–900 m, fide Bernardi). At La Grille, I found it to be locally abundant and codominant as a subcanopy or canopy tree, striking when in fruit with numerous, large brown receptacles hanging from the trunk and branches, some split open to reveal an array of red-orange carpels set against a pale orange background. One of the largest known members of the genus, both in habit and in fruit, it flowers from August to December concurrently with the ripening of the previous year's fruit crop.

GRANDE COMORE. NTSORALE DIMANE: 250–900 m, *Nuxia* and *Weinmannia* formation, 9 Dec. 1967 (fl), *Bernardi 11803* (G, 2 sheets; K, P, Z). LA GRILLE: 850–900 m, *Tambourissa, Ocotea, Anthocleista,* and *Polyscias* formation, 1–3 Dec. 1967 (fl, fr), *Bernardi 11645* (G, 2 sheets; K, P, Z); May 1963 (fl), *Bosser 18096*

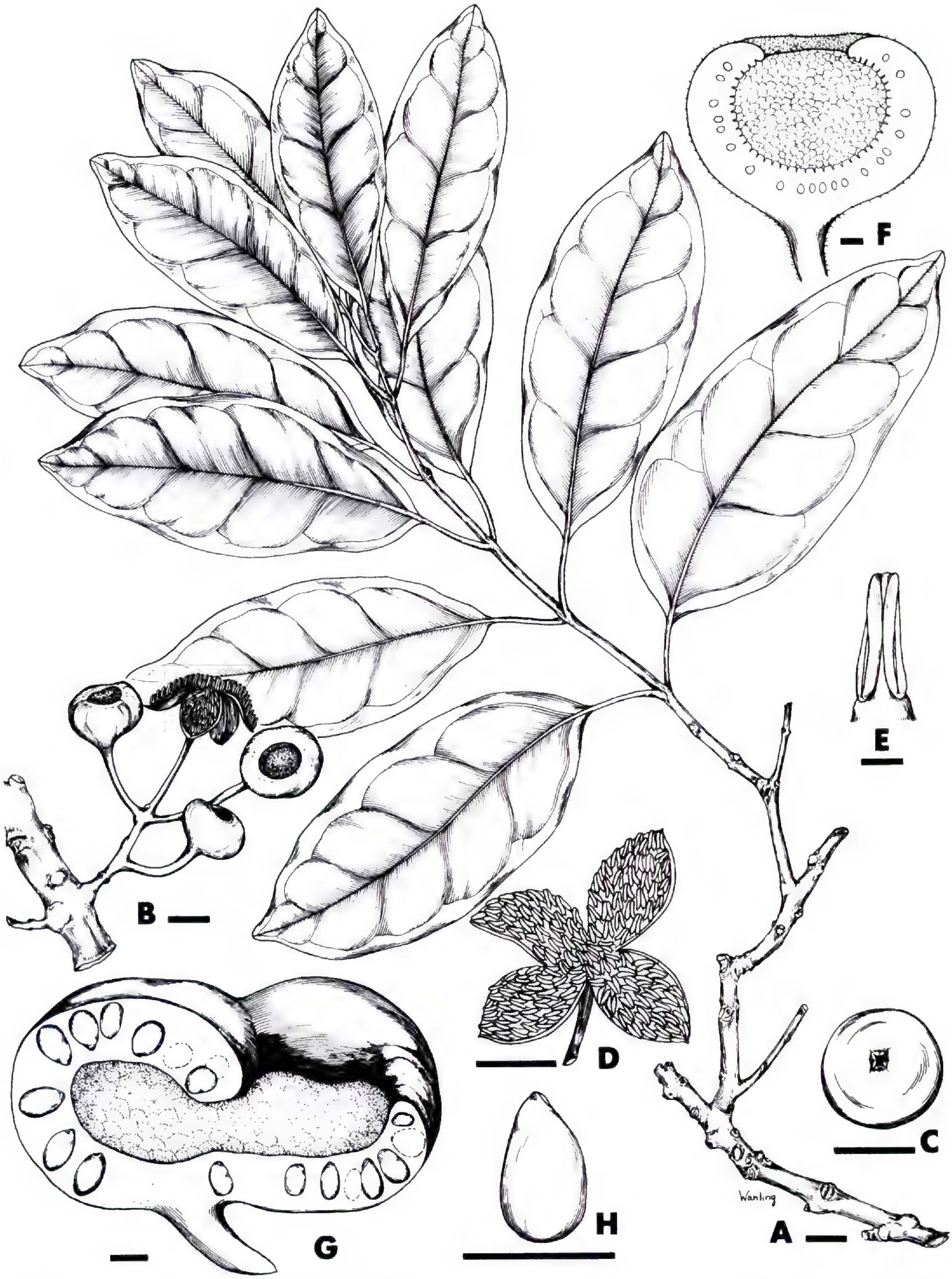


FIGURE 34. *Tambourissa comorensis* Lorence.—A. Habit.—B. Inflorescence with androecious and gynoecious flowers.—C. Androecious flower in bud, apical view.—D. Androecious flower at anthesis, apical view.—E. Stamen, adaxial view.—F. Gynoecious flower, longitudinal section.—G. Submature fruiting receptacle, longitudinal section.—H. Fruiting carpel, lateral view. All *Lorence 2878* (MO). Bars equal 10 mm in A–D, G, H, and 1 mm in E, F.

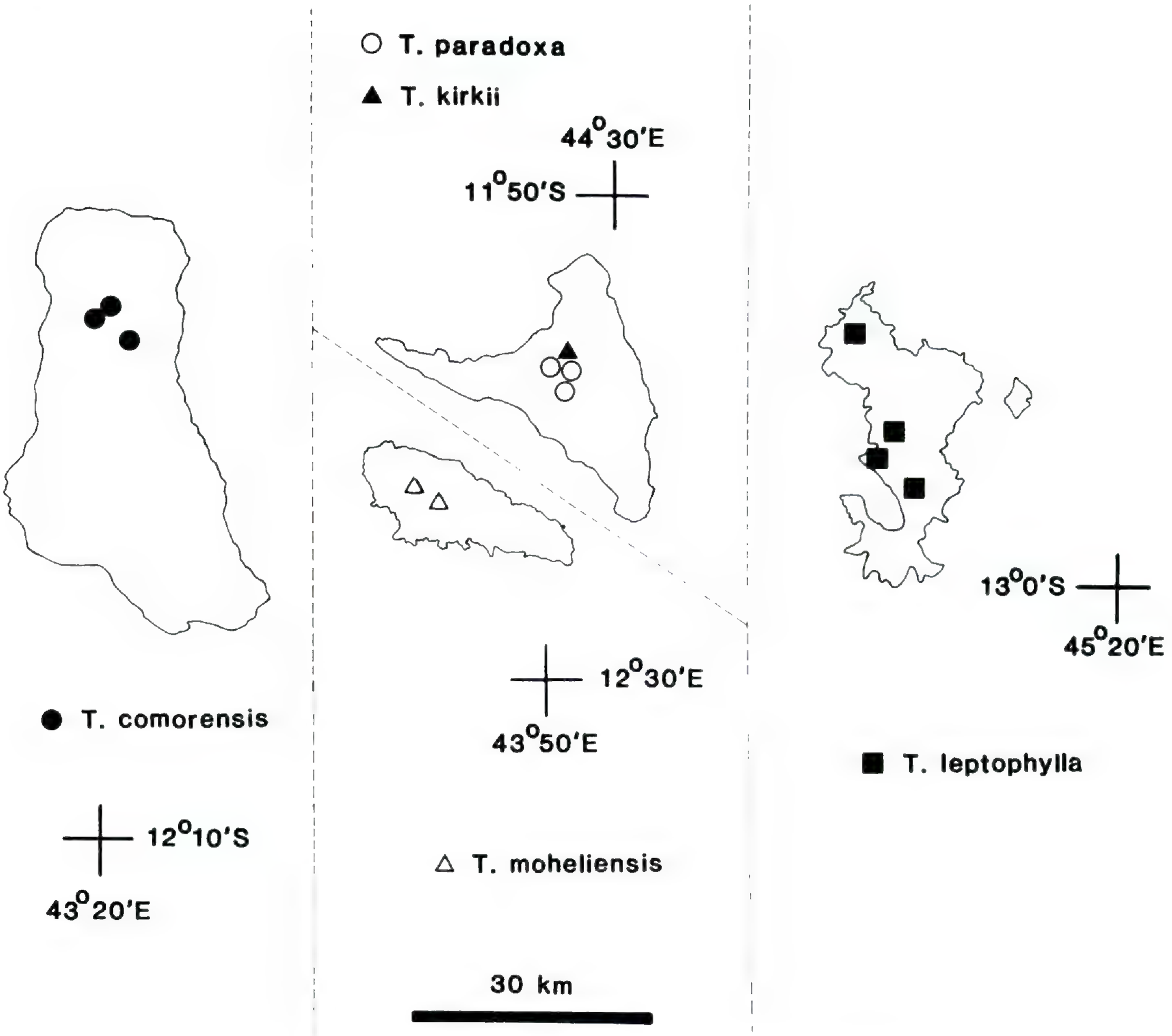


FIGURE 35. Distribution maps of *Tambourissa* in the Comore Islands (left to right): Grande Comore, Mohéli, Anjouan, Mayotte.

(MAD, P); ca. 800 m, 29 July 1979 (fr), *Lorence & Banfi 2877* (MO, K, P); 9 Feb. 1957 (fl), *Anon. in SF-16529* (P).

Tambourissa comorensis belongs to species Group 2A, also including *T. leptophylla* which differs by its smaller androecious buds, fewer stamens, and by its gynoecious receptacle with a much smaller orifice and acute, conical styles. Also, fruits of the latter are uniformly dull, corky brown externally with a smaller orifice. Dried fruits of *T. comorensis* are strongly fragrant in the herbarium, like those of *T. moheliensis* (Group 3). *Tambourissa kirkii* (Group 2B) differs by its small, globular androecious flowers, which open only partially and contain fewer stamens with acute, prolonged connectives. In living material, androecious flowers of *T. comorensis* are white and produce a pleasant, sweet odor of fermenting fruit. Buds and gynoecious flowers are pale green externally. At anthesis, gynoecious flowers have glistening, pale green styles, although massive mucilage production was not apparent. In mixed inflorescences of *Lorence & Banfi 2788,* the gynoecious flowers matured before the androecious flowers.

Vernacular name and uses. M'Bweza (Grande Comore), meaning "to calm the pain" or "to heal." Natives of Grande Comore infuse the leaves to make a medicinal tea.

16. Tambourissa leptophylla (Tul.) A.DC., Prodr. 16(2): 658. 1868; Baill., Hist. Pl. ed. 2, 1: 310, 344, 345. 1871; Cavaco in Humbert, Fl. Madagascar 80: 34, fig. VIII:1–4. 1959. *Ambora leptophylla* Tul., Ann. Sci.

Nat. (Paris) 4(3):29. 1855; Tul., Monogr. Monim. 298, tab. 25, fig. 1. 1855. TYPE: Comore Archipelago. Mayotte: Zuaby (ca. 1851) (fl), *Boivin 3133* (lectotype, P, here designated; isolectotypes, P, 4 sheets).

Monoecious or subdioecious tree attaining 10 m tall and 40 cm D.B.H., the bark pale brown, flaking, the new growth finely pubescent, the mature leafy stems glabrescent, terete, 3–5 mm diam. Leaves opposite to subopposite, glabrous, petiolate; petiole 15–20 mm by 1.5–2.5 mm; lamina membranaceous to chartaceous, ovate to elliptic or oblong, 120–250 mm by 60–110 mm, the apex shortly acuminate to acute, the base acute to obtuse, often slightly decurrent, the secondary veins 5–8 pairs, making a 50–65° angle with the costa, the venation visible to 4° adaxially and to 4(–5°) abaxially, the margin plane to slightly revolute; juvenile and sucker leaves heterophyllous, the margin serrate with 2–5 pairs of teeth in the apical half, the petioles red when living. Inflorescence a pleiochasium or thyrse of 7–25 flowers, sometimes leafy, cauliflorous from meristematic swellings on the trunk, or a ramiflorous pleiochasium of 5–11 flowers on the leafless nodes, or the flowers solitary and axillary, when young finely velutinous, later puberulent, the floral axis 20–150 mm by 1–3 mm, subtended by several minute, caducous bracteoles. Androecious flower in bud globose-depressed, 6–8 mm diam., smooth, the apex with 4 minute puberulent tepals, the pedicel 10–40 mm by 1–1.5 mm, subtended by a small, velutinous deltoid bracteole; at anthesis deeply 4-fid, 20–25 mm diam., the lobes spreading flat, the internal receptacle surface glabrous; stamens 80–90, linear-ligulate, recurved, 2–3 mm long by 0.8–1 mm wide, the loculi separate, parallel, occupying almost the entire length of the stamen, apically connivent or the connective slightly prolonged and apiculate. Gynoecious floral receptacle globose-patelliform, apically depressed; at anthesis 10–15 mm diam. by 5–7 mm long, the orifice entire, circular, comprising ca. ¼–⅓ total width of the receptacle, open even in bud, the rim hirsute; styles very numerous, ca. 300–600, broadly conical, 0.6–0.8 mm long by 0.3–0.5 mm wide basally, the internal receptacle surface hirsute between the styles. Fruiting receptacle solitary or in clusters of 2–4 on the trunk and major branches, globose-patelliform, apically depressed, 90–130 mm diam. by 75–90 mm long, the orifice circular, entire, 15–40 mm diam., comprising ca. ⅙–¼ total width of the receptacle, the walls 16–25 mm thick, the external surface uniformly dull, corky grayish brown, the internal surface with scattered, sharply conical styles 0.7–1 mm long by 0.5–0.8 mm wide basally, interspersed with abundant simple hairs, the pedicel and peduncle tapered, 70–80 mm long by 9–10 mm diam. medially. Mature carpels ovoid-compressed, 13–17 mm long, 8–10 mm wide, 3–6 mm thick, the endocarp light to dark brown, the surface shallowly foveolate-reticulate.

Distribution. Endemic to Mayotte, Comore Archipelago (Fig. 35).

Habitat. It is local and occasional in lower montaine evergreen wet forest formations often dominated by *Aphloia* and *Nuxia*. Recent collections are from the Benara massif (400–653 m) and also the Hachiroungou massif (400–600 m), in remnants of indigenous forest. The species also occurs in secondary forest with native remnants, the recent collections being from Barakani and Sada, both at ca. 100 m. Flowering occurs from August to September concurrently with the ripening of last year's fruits.

MAYOTTE. BARAKANI: secondary forest and along roadside, ca. 100 m, 24 July 1979 (fr), *Lorence & Saida 2824* (MO); near Barakani, Aug. 1977 (fl, fr), *Tattersall s.n.* (MO). BENARA MASSIF: E peak, wet forest on summit, ca. 600–653 m, 24 July 1979 (st), *Lorence & Saida 2828* (K, MO); (fl), *Lorence & Saida 2829* (MAU, MO, P). DZOMNOGNE: (fl), *Pobeguin 86* (P). HACHIROUNGOU MASSIF: (NW Mayotte) wet forest with *Nuxia* and *Aphloia*, ca. 400–500 m, 26 July 1979 (fr), *Lorence & Saida 2854* (K, MAU, MO, P, REU, Z). SADA: ca. 100 m, Aug. 1977 (fl), *Tattersall s.n.* (MO).

Tambourissa leptophylla belongs to species Group 2A. Its androecious flowers most closely approach those of *T. comorensis*, which also split into four flat segments and bear numerous stamens with long anthers, although flowers and buds of the latter are larger. Gynoecious flowers of *T. leptophylla* have acutely conical styles as in *T. kirkii* (Group 2B), but androecious flowers of the latter are much smaller, open only partially, and have fewer stamens (ca. 50) with short, medial loculi and acutely prolonged connectives. All three species are presumably derived from a common ancestor, perhaps one similar to *T. madagascariensis*.

Vernacular name. Ambora (Mayotte).

17. Tambourissa kirkii Cavaco, Kew Bull. 12(2): 228. 1957; Cavaco, Bull. Soc. Bot. France

104: 284, fig. 3. 1957. TYPE: Comore Archipelago. Johanna (Anjouan): without precise locality, Zambesi Expedition, 1,000 ft. (ca. 300 m), small tree, Aug. 1862 (fl, fr), *Kirk s.n.* (holotype, K) (see also Kirk's fig. 355, with type).

Monoecious shrub or small tree, the new growth hirsutulous, the mature leafy stems glabrous, stramineate, 2.5–4 mm diam. Leaves opposite to subopposite, glabrous, petiolate; petioles 10–15 mm by 1–1.5 mm; lamina ovate to elliptic, 100–135 mm by 55–70 mm, the apex shortly acuminate, the base obtuse to rounded, the secondary veins 6–7 pairs, making a 50–55° angle with the costa, the venation visible to 3–4° on both surfaces, the margin slightly revolute. Androecious inflorescence unknown. Androecious flower (from Kirk's fig. 355) globose, ca. 9–10 mm diam.; at anthesis deeply 3-fid, opening slightly, the lobes incurved; stamens probably ca. 50, subulate, ca. 3–4 mm long by 0.5 mm wide, the loculi separate, lateral, occupying medial ⅓ of stamen, the filament basally broad, comprising ca. ⅓ total length of the stamen. Gynoecious inflorescence a 4(–5)-flowered, finely velutinous pleiochasium, the position unknown, the floral axis ca. 20 mm by 1.5 mm, bearing rare, scattered bracteoles; female floral receptacle cupuliform-patelliform, 8–12 mm diam. by 5–6 mm long, the orifice broad, circular, entire, comprising ca. ¾ total width of the receptacle, the rim velutinous, the external surface finely velutinous, ± pustular; styles numerous, ca. 200, broadly conical, apiculate, 0.5–1 mm long by 0.5 mm diam. basally, bearing short, scattered hairs, the internal receptacle surface velutinous between the styles. Fruiting receptacle (from Kirk's fig. 355) broadly cupuliform-patelliform, ca. 250–300 mm diam., the broad, subcircular orifice comprising ca. ⅓–⅔ total width of the receptacle, the conical styles persistent in fruit. Mature (?) carpels ca. 10–12 mm long by 7–8 mm wide, ovoid-compressed, the endocarp "black and hard, surrounded with a red fleshy body" (fide Kirk).

Distribution. Endemic to Anjouan (Fig. 35).

Habitat. According to the information given on the label, *Tambourissa kirkii* occurs at 1,000 ft. (ca. 300 m), but on his figure 355 (an unpublished pencil drawing), Kirk notes "shrub growing at height of 2,000 feet (ca. 600 m) . . . seeds said to be cathartic. Monoecious." It probably occurs in montane wet forest.

Tambourissa kirkii belongs to species Group 2B. As noted by Cavaco (1957a), it is closely allied to *T. leptophylla* (Group 2A) from neighboring Mayotte. The latter differs by its more sparsely pubescent inflorescence, smaller gynoecious floral and fruiting receptacle orifice, glabrous styles, and by its androecious flower which is about twice as large with more numerous stamens having much longer loculi extending for almost the entire length of the stamen, and a scarcely prolonged connective.

Tambourissa paradoxa (Group 2B), also from Anjouan, has smaller, globular androecious flowers opening by a small pore and structurally similar stamens: it may even be conspecific with *T. kirkii*. As gynoecious flowers are unknown in the former, however, and androecious flowers of the latter are known only from a single pencil sketch, I have decided to recognize both species until further data and collections become available. *Tambourissa comorensis* and *T. leptophylla* differ by the characters mentioned above.

18. Tambourissa paradoxa Perk., Pflanzenr. 4, 101 (Nachtr.): 43. 1911. TYPE: Comore Archipelago. Johanna (Anjouan): without precise locality (fl), *Anon. sub Herb. Blackburn s.n.* (possibly *Bojer*) (holotype, K).

T. johannae Perk., Pflanzenr. 4, 101 (Nachtr.): 43. 1911. TYPE: Comore Archipelago. Johanna (Anjouan): Zylangi Lake, 27 Oct. 1862 (fl), *Anon. sub Zambesi-Expedition s.n.* (possibly *Kirk*) (holotype, K, lefthand specimen with flowers).

Monoecious shrub or small tree attaining 10 m tall, the new growth unknown, the adult leafy stems glabrous, terete, 3–4 mm diam., yellowish brown. Leaves opposite to subopposite, glabrous, petiolate; petioles 10–20 mm by 1–1.5 mm; lamina chartaceous, elliptic to ovate elliptic, 60–140 mm by 25–50 mm, the apex acute to acuminate, the base acutely cuneate to acutely decurrent, the secondary veins 5–8 pairs, making a 40–45° angle with the costa, the venation prominent and visible to 3° adaxially and to 4° abaxially, the margin moderately revolute. Androecious inflorescence ramiflorous, a sparse, puberulent pleiochasium of 3–11 flowers, or the flowers solitary and axillary, the floral axis 6–12 mm by 1 mm, bearing scattered, simple hairs, subtended by several pairs of minute, ciliate deltoid bracteoles. Androecious flower in bud globose, the pedicel 5–12 mm by 0.6–1 mm, bearing a few sparse hairs, subtended by 1(–2) minute,

caducous deltoid bracteoles; at anthesis globose, 4–8 mm diam., not splitting but opening by a shallowly 4-lobed apical orifice ca. 2 mm diam. flanked by 4 small, decussate, obtusely deltoid ciliate tepals ca. 0.6–1 mm wide by 0.3–0.5 mm long, the internal surface of each lobe bearing 2–10 fleshy, obtuse to deltoid tepals intergrading with the stamens; stamens ca. 40–50, subulate-lanceolate, 2–3 mm long by 0.5–0.8 mm wide, the loculi lateral, separate, occupying basal ⅔ of stamen, the connective prolonged, acuminate, slightly exserted from the orifice at anthesis; internal receptacle surface glabrous. Gynoecious flowers unknown. Fruiting receptacle solitary on leafless branches, shallowly cupuliform, 53–150 mm diam. by 25–50 mm long, externally corky, the orifice comprising ca. ½ total width of receptacle, the internal surface with numerous broadly conical styles 0.7–0.8 mm long, more or less glabrous in between; pedicel and peduncle 15–17 mm by 5–7 mm. Mature carpels ovoid-compressed, 11 mm long by 6 mm wide.

Distribution. Endemic to Anjouan (Fig. 35).

Habitat. The species is apparently restricted to evergreen montane wet forest from ca. 650 to 1,400 m, according to available information.

ANJOUAN. WITHOUT PRECISE LOCALITY: Traprock (?) soils of hills, 2,000–3,000 ft., 29 Oct. 1862 (st), *Anon. sub Zambesi Expedition s.n.* (possibly *Kirk*) (K, sterile right hand specimen, not a type); (fl), *Levanché 21* (P); Oct. 1902 (fl, fr), *Levanché s.n.* (P); forêts, May 1850 (st), *Boivin s.n.* (P). N'TNIGUE PEAK: 4,200 ft. (ca. 1,400 m), in evergreen forest, food of pigeons, bulbuls and thrushes, tree ± 20 ft. tall with huge fruits hanging on stem filled with orange covered black seeds, 2 Oct. 1958 (fr), *Benson 142* (BM).

The types of *Tambourissa johannae* and *T. paradoxa* are both from Anjouan. Both collections have morphologically similar leaves, small, globular androecious flowers which open by a narrow apical orifice flanked internally by decussate, scale-like tepals, and have virtually identical stamens containing oil cells and a few sclerids, but lacking tanniferous idioblasts. It seems clear that these two concurrently published taxa are conspecific. I have chosen to retain the epithet *paradoxa*, as its type possesses more numerous and mature flowers than the type of *T. johannae*. *Tambourissa paradoxa* is an imperfectly known species and further field observations and collections, particularly of female flowers and fruit, are desired.

As is the case for *Tambourissa gracilis* and *T. purpurea* (both Madagascar), the androecious flowers of *T. paradoxa* open by small apical pores. Unlike the stamens of the former two, which are nearly sessile with apically confluent loculi, those of *T. paradoxa* are long and lanceolate with separate, lateral loculi and acute, prolonged connectives.

A close affinity appears to exist between *Tambourissa paradoxa* and *T. kirkii* (also Anjouan), which has strikingly similar floral and staminal morphology, although androecious flowers of the latter species split into 3–4 segments and lack the exserted connectives of the former. Both belong to species Group 2B. Similar androecious floral and staminal morphology occurs in *T. moheliensis* (Group 3) from neighboring Mohéli, although here the loculi are united basally into a U-shape, and the gynoecious flower differs in being closed in bud. The similarities in androecious floral and staminal morphology of *T. paradoxa, T. kirkii,* and *T. moheliensis* may be a result of convergence to accommodate similar pollinators, as the very different gynoecious flower of the latter suggests a closer affinity to the Madagascan *T. capuronii* (also Group 3).

Vernacular name. M'Bweza (Anjouan, fide *Benson 142,* BM).

19. Tambourissa moheliensis Lorence, Bull. Mus. Hist. Nat. (Paris), Ser. 4, Sect. B, Adansonia 3(3): 300, pl. 2, figs. 9–11. 1982. TYPE: Comore Archipelago. Mohéli: mountains between Fomboni and Drodoni, low montane forest, 500–700 m, 6 Dec. 1967 (fl, fr), *Bernardi 11781* (holotype, Z; isotypes, G, K, P).

Monoecious or subdioecious tree 4–15 m tall by 70 cm diam., the new growth glabrous or with sparse, scattered hairs, the mature leafy stems pale green, terete, 2–5 mm diam. Leaves opposite to subopposite, glabrous, petiolate; petioles 7–22 mm by 1–1.5 mm; lamina subcoriaceous, ovate, broadly to narrowly elliptic, oblong or rarely obovate, 45–220 mm by 30–70 mm, the apex acute to acuminate, rarely rounded, the base acute to obtuse, cuneate or decurrent, rarely obtuse or rounded, the secondary veins 4–8 pairs, making a 45–65° angle with the costa, the venation visible to 2(–3°) adaxially and to 3(–4°) abaxially, the margin slightly revolute. Gynoecious inflorescence a finely pubescent, cauliflorous pleiochasium or thyrse of up to 20 flowers; androecious inflorescence a ramiflorous plei-

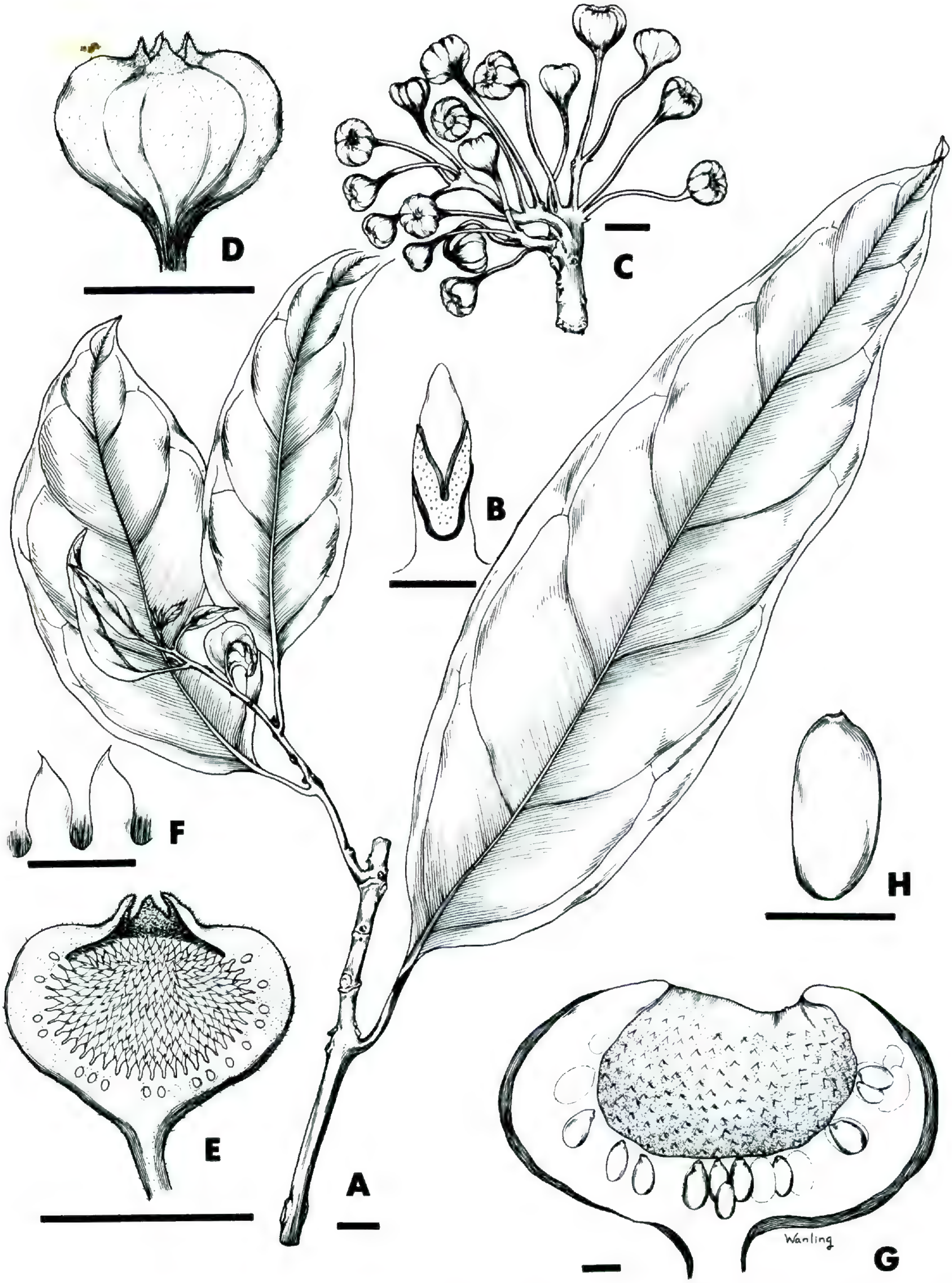


FIGURE 36. *Tambourissa moheliensis* Lorence.—A. Habit.—B. Stamen, adaxial view.—C. Submature gynoecious inflorescence.—D. Gynoecious flower at anthesis, lateral view.—E. Gynoecious flower, longitudinal section.—F. Styles, lateral view.—G. Submature fruiting receptacle, longitudinal section.—H. Fruiting carpel, lateral view. A–E. *Bernardi 11781* (G). F. *Bernardi 11759* (G). G, H. *Bernardi 11781* (Z). Bars equal 10 mm in A, C–E, G, H, and 1 mm in B, F.

ochasium of ca. 5 flowers on the leafless nodes, or the flowers solitary and axillary or rarely subterminal on short leafy shoots; floral axis 15–70 mm by 1–5 mm, finely pubescent or with scattered simple and fasciculate hairs, subtended by several ciliate-velutinous deltoid bracteoles. Androecious flower in bud globose, 4.5–6 mm diam., apiculate with 4 minute, decussate velutinous tepals, the pedicel 10–12 mm by 0.8 mm, bearing scattered hairs, subtended by a minute, deltoid caducous bracteole; at (complete?) anthesis globose, 5–6 mm diam., splitting into 4 shallow, inflexed lobes, each with 3–4 obtuse, scale-like tepals apically on the internal surface, these intergrading with the stamens, the internal receptacle surface glabrous; stamens ca. 50, narrowly acute to subulate, 2–2.5 mm long by 0.6–0.8 mm wide basally, the loculi subparallel, occupying ca. ⅔ total length of stamen, usually united basally into a single, U-shaped loculus, rarely free, the filament short, broad, the connective acute, prolonged. Gynoecious flower in bud napiform-depressed, pubescent, apiculate with 4 velutinous deltoid tepals 0.5 mm wide, the pedicels 20–40 mm by 1.5–2 mm, pubescent; at anthesis napiform-depressed, 12–16 mm diam. by 7–10 mm long, the orifice X-shaped, 1–2 mm wide, opening by 4 straight to suberect deltoid lobes, these finely pubescent-velutinous on both surfaces; styles numerous, ca. 100–200, conical, slightly ventricose medially, 1–1.3 mm long by 0.3–0.5 mm wide basally, glabrous, the internal receptacle surface velutinous with dense, simple and fasciculate hairs between the styles. Fruiting receptacle borne on the trunk, patelliform to napiform or subglobose, depressed, ca. 120 mm diam. by 70–75 mm long, the internal surface uniformly pale, corky gray-brown, the orifice comprising ca. ½ total width of receptacle, subentire, bearing remnants of the black, deltoid lobes, the walls ca. 20–26 mm thick, the internal surface bearing numerous scattered, narrowly conical, angular styles 1–1.5 mm long by 0.8–1 mm wide basally, interspersed with scattered to dense, simple and fasciculate hairs. Mature carpels ellipsoid to ovoid, compressed, 12–15 mm long, 6–7 mm wide, 4–5 mm thick, the endocarp dark brown, the surface scrobiculate. Figure 36.

Distribution. Endemic to Mohéli, Comores (Fig. 35).

Habitat. The species occurs in montane evergreen forest from ca. 500 to 700 m. Both flowers and fruits are produced in December.

MOHÉLI. FOMBONI: Bamboa, forest, 8 Mar. 1957 (fl), *Anon. in SF-16731* (P). MT. ST. ANTONIO: 600–700 m, in montane and submontane forest, 5 Dec. 1967 (fl, fr), *Bernardi 11759* (G, K, P, Z).

Mohéli, smallest of the four Comores, is probably also the most poorly explored botanically, with only three collections of *Tambourissa* known from the island. After much deliberation I have decided to treat all as a single species, although more extensive collections and field observations are required to ascertain whether or not they are truly conspecific.

The first collection, *Bernardi 11781,* possesses two gynoecious inflorescences with numerous flowers and a single submature fruit. Because it has numerous flowers in both thyrses and pleiochasia in addition to the fruit, I selected it as the type. *Anon. in SF-16731,* from the same locality, corresponds well with the type vegetatively, but the buds are unfortunately immature.

The third collection from Mohéli, *Bernardi 11759,* differs in having nearly glabrous new growth, smaller and more shortly acute or apically rounded leaves with fewer secondary veins oriented at a greater angle to the costa, and stronger, more distinct secondary vein arches. The more sparsely pubescent androecious flowers are in short, ramiflorous pleiochasia of up to five flowers, or rarely solitary and axillary or subterminal. Apart from the fact that the anther loculi are basally confluent in *Bernardi 11759* (Fig. 36B), the narrowly acute to subulate stamens with long connectives and closed, globular androecious flowers most closely resemble those of *T. kirkii* and *T. paradoxa* from nearby Anjouan, except that they contain dark tanniferous idioblasts. In terms of androecious floral and staminal morphology, *Bernardi 11759* could represent an undescribed species. The specimen at Geneva, however, has a single corky brown immature fruit with the orifice bearing six deltoid lobes that corresponds well with *Bernardi 11781,* and for this reason I tentatively consider them conspecific.

On the basis of androecious floral and staminal morphology, *Tambourissa moheliensis, T. kirkii,* and *T. paradoxa* would appear to be derived from a common ancestor. However, unlike the female receptacles of *T. kirkii, T. comorensis,* and *T. leptophylla* (all Group 2), which all have a circular, entire orifice open even in bud, that of *T. moheliensis* is closed in bud and splits open by four, deltoid segments as in *T. capuronii* (Madagascar). Moreover, the floral ground tissue

of both the latter species contains numerous dark brown tanniferous idioblasts not found in the other Comorean species. These characters suggest that *T. moheliensis* was derived from a different ancestor than the other Comorean species and appears most closely allied to *T. capuronii* with which I have placed it in species Group 3.

Vernacular name. Diarou.

20. Tambourissa capuronii Cavaco, Bull. Mus. Hist. Nat. (Paris), Ser. 2, 29: 287. 1957; Cavaco in Humbert, Fl. Madagascar 80: 20, fig. VI:5–8. 1959. TYPE: Madagascar. Diego Suarez: Betsomanga Massif, valley on the S flank, ca. 550 m, 17 Nov. 1950 (fl), *Capuron 820-SF* (holotype, P; isotype, P).

Large monoecious tree 25–30 m tall and 40–60 cm D.B.H., the new growth hirtellous, the mature leafy stems glabrous, petiolate; petioles 12–30 mm by 1.2–1.5 mm; lamina chartaceous to subcoriaceous, abaxially hirtellous to glabrate, elliptic to oblong or obovate, (68–)90–165 mm by 30–74 mm, the apex shortly acuminate, acute or rarely obtuse, the base cuneate to acute, rarely obtuse, the secondary veins 7–10 pairs, making a 55–65° angle with the costa, the venation prominent, visible to 4° on both surfaces, the margin moderately revolute. Inflorescence a cauliflorous, unisexual or sexually mixed pleiochasium of 4–15 flowers, or rarely a fascicle of 2–3 flowers, all parts corky brown externally, the floral axis 10–170 mm by 1–5 mm. Androecious flower in bud globose, 15–19 mm diam., corky brown, slightly apiculate with coalescent tepals, the pedicel 28–55 mm by 2–2.5 mm; at anthesis deeply 4(–5)-fid, 40–55 mm diam., the lobes spreading flat; stamens numerous, ca. 300, lanceolate, 6–8 mm long by 1–1.5 mm wide basally, subsessile, the loculi narrow, separate, lateral, occupying the basal ¾–⅘ of stamen, the filament short or lacking, the connective acuminate, slightly prolonged, comprising apical ¼–⅕ of stamen, the apex sometimes bearing up to 5 simple hairs, the internal receptacle surface glabrous or with scattered simple hairs. Gynoecious flower in bud napiform-depressed, corky brown, 15–20 mm diam.; at anthesis to 35 mm long by 40 mm wide, the apex splitting into ca. 6 thick, irregularly deltoid lobes; styles numerous, ca. 200–300, narrowly conical, slender, 4–5 mm long by 0.5 mm wide basally, solitary or coalescent into groups of up to 12, the internal receptacle surface densely pilose between the styles and around the orifice; pedicel to 75 mm by 5 mm. Submature fruiting receptacle cupuliform, externally corky, 35 mm long by 55 mm diam., the carpels ovoid-compressed, to 13 mm by 8 mm.

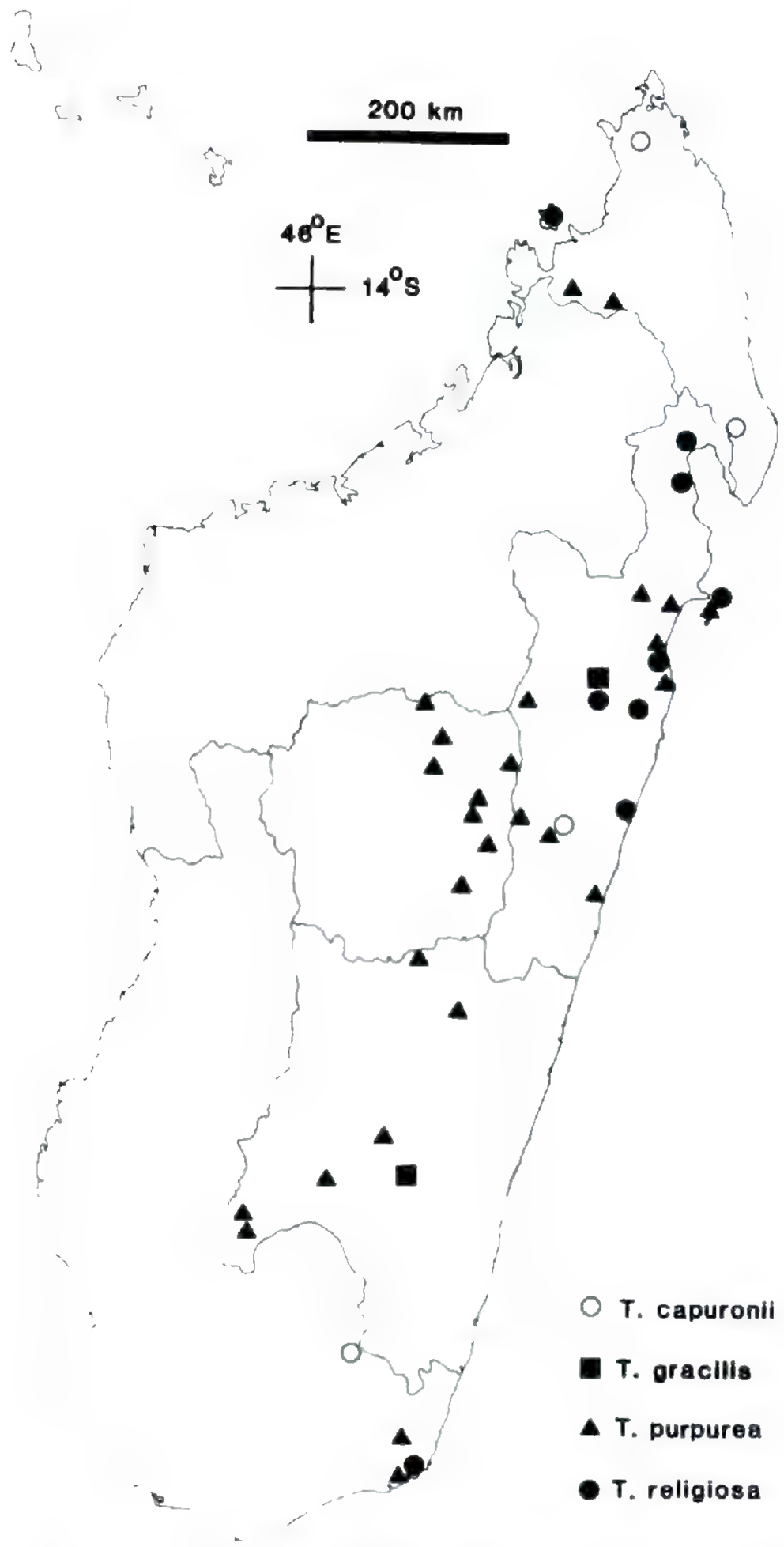


FIGURE 37. Distribution map of some *Tambourissa* species in Madagascar.

Distribution. Endemic to Madagascar (Fig. 37).

Habitat. Contrary to Cavaco's original (1957d) statement that the species was a highly restricted endemic, his subsequent list of exsiccata (1959) shows *Tambourissa capuronii* to be fairly widely distributed both in lowland Myristicaceae/*Anthostema* wet forest from ca. 300 to 800 m, and also in *Tambourissa*/*Weinmannia* montane wet forest from ca. 800 to 1,400 m, ranging from Mt. D'Ambre (Diego Suarez) in the north, south along the eastern escarpment, to the Mandrare River near Fort Dauphin in the southeast. The species was said by Capuron to be very abundant in 1950 at Betsomanga between 350

and 600 m. A canopy tree reaching ca. 30 m, it flowers in November–December and is one of the largest members of the genus.

MADAGASCAR. DIEGO SUAREZ: forêt d'Ambre, 1,200 m, Sept. 1926 (fl), *Perrier de la Bâthie 11741* (P). TAMATAVE: Analamazaotra forest (Perinet) 800 m (fl), *Perrier de la Bâthie 10087* (P); *Perrier de la Bâthie 10095* (P); Antasibe, Soanierana, E coast, 350 m, 10 Dec. 1938 (fl), *Lam & Meeuse 5835A* (P). TULEAR: upper basin of the Mandrare River (SE), pass and summit of Marosoui, forest on gneissic laterite, 1,000–1,400 m, 14–15 Nov. 1928 (fl), *Humbert 6606* (B, G, 2 sheets; K, MAD, P).

Tambourissa capuronii appears to be most closely related to the Comorean *T. moheliensis* with which it comprises species Group 3. The latter is distinguishable by its much smaller Androecious flowers and stamens, and styles which are never coalescent into groups as in *T. capuronii*. None of the other Madagascan species appears to be closely allied to *T. capuronii*.

21. Tambourissa religiosa (Tul.) A.DC., Prodr. 16(2): 659. 1868; Perk. & Gilg, Pflanzenr. 4, 101: 71. 1901; Drake in Grandidier, Hist. Phys. Madagascar 1(1): 23. 1902; Perk., Pflanzenr. 4, 101 (Nachtr.): 44. 1911; Cavaco in Humbert, Fl. Madagascar 80: 36. 1959, excluding fig. X:5 (which is *T. elliptica* subsp. *micrantha*). *Ambora religiosa* Tul., Ann. Sci. Nat. (Paris) 4(3): 30. 1855; Tul., Monogr. Monim. 30, pl. XXVII. 1855. TYPE: "Bourbon" (Réunion). (Fide Richard, but probably Madagascar), ca. 1851 (fl), *Boivin s.n.* (lectotype, P, here designated).

Ambora tamburissa Boiv. ex Tul., Monogr. Monim. 303. 1855, non Lam. ex Steud.

Tambourissa boivinii A. DC., Prodr. 16(2): 659. 1868; Perk & Gilg, Pflanzenr. 4, 101: 70. 1901; Drake in Grandidier, Hist. Phys. Madagascar 1(1): 23. 1902; Perk., Pflanzenr. 4, 101 (Nachtr.): 42. 1911. TYPE: Madagascar. Tamatave: Sainte Marie Island, Lafondroa forest, Mar. 1847 (fr), *Boivin 1728* (holotype, P).

Tambourissa quadrifida sensu Drake in Grandidier, Hist. Phys. Madagascar 1(1): 21. 1902, pro parte (as to *Baron 2504*), non Sonnerat.

Monoecious shrub, treelet, or small tree 4–5 m tall, the new growth glabrous, the mature leafy stems ascendant, dark brown to stramineate, 2.5–6 mm diam. Leaves opposite to subopposite, glabrous, petiolate; petioles (10–)15–30 mm by (1–)1.5–2.5 mm; lamina subcoriaceous to coriaceous, ovate elliptic, elliptic, oblong, narrowly oblong or obovate, 70–150(–175) mm by (16–)30–60 mm, the apex shortly acuminate, bluntly acute, obtuse or retuse, the base acute, cuneate or obtuse, often ± decurrent, the secondary veins 6–10 pairs, making a 60–70° angle with the costa, the venation obscure or visible to 2–3° adaxially, visible to 3–4° abaxially, the intramarginal loops uniting to form a conspicuous, partial marginal fimbrial vein, the margin thickened, moderately to strongly revolute. Inflorescence glabrous, either a terminal, axillary, or ramiflorous dichasium of 3 flowers or condensed pleiochasium of 5–7 flowers (the gynoecious flower terminal, if present), or the flowers solitary and terminal or axillary, the floral axis 1–7 mm by 1.5–2 mm, the axis and pedicels subtended by several glabrous to sparsely ciliate, broadly deltoid bracteoles with pale margins. Androecious flower in bud blackish to yellowish, globose to napiform, 7–10 mm diam. by 4–6 mm long, ± depressed, apiculate with 2–4 minute, deltoid glabrous tepals, the pedicel 3.5–5 mm by 1–1.5 mm; at anthesis unknown, presumably splitting into 4 shallow lobes (as in *T. purpurea*); stamens in bud ca. 60–82, linear-ellipsoid to slightly ovoid, 0.8–1 mm long by 0.5–0.7 mm wide, the filament short, distinct, slender, the loculi lateral, separate (rarely confluent apically), the connective rarely prolonged into an apicule, the internal surface with sparse hairs. Gynoecious flower in bud napiform-depressed, the pedicel 6–7 mm by 1–1.5 mm; at anthesis 8–11 mm diam. by 5–7 mm long, the orifice shallowly 4-lobed, X-shaped, 0.5–1.5 mm wide, the walls thick; styles numerous, ca. 300, conical, acuminate, slightly ventricose, 0.5–1.7 mm long by 0.3–1.5 mm wide basally, the internal receptacle surface with clusters of simple hairs between the styles. Fruiting receptacle terminal, solitary, or rarely paired, napiform-depressed to subglobose, to 52 mm diam. by 40 mm long, the external surface smooth, dark brown with corky patches, the orifice ca. 12 mm diam., comprising ¼–⅕ total width of receptacle, subcircular, subentire, the walls 10–17 mm thick, the internal surface with scattered conical-columnar styles 0.3–0.5 mm long and wide basally, interspersed with scattered hairs. Mature (?) carpels ovoid-compressed, 7–9 mm long, 5–6 mm wide, 4–5 mm thick, the endocarp light brown to beige, the surface shallowly scrobiculate.

Distribution. The species is endemic to Madagascar. Cordemoy (1895) erroneously cites the species as occurring in Réunion, but was actually referring to *Tambourissa crassa* (q.v.). The lec-

totype of *T. religiosa* was said by Richard to have come from Bourbon (Réunion), but this is undoubtedly due to a mixup in herbarium labels, because his other collections of the species are all from Madagascar and no other authentic specimens are known from Réunion (Fig. 37). It was selected because it represents the best of the four syntypes. The type of *T. boivinii,* although in poor condition, is clearly referable to *T. religiosa.*

Habitat. In Madagascar *Tambourissa religiosa* appears to be commonest in the eastern littoral forests where it occurs sympatrically with *T. purpurea.* The species ranges inland to the mountainous central plateau from altitudes of 1,500 to 1,700 m, and across the northwestern region to the offshore island of Nosy Be.

MADAGASCAR. DIEGO SUAREZ: Nossi Be, 23 July 1840 (st), *Perville 295* (P, syntype); 10 Oct. 1840 (fr), *Perville 328* (P, syntype). TAMATAVE: Ambila, 1 May 1928 (fl), *Decary 6288* (MAD, P); 10 May 1928 (fl, fr), *Decary 6554* (K, MAD, P); Rantabe, N of Tamatave, littoral forest, 1 June 1969 (st), *Guillaumet 3002 bis* (MAD); Maroa, forests within Antongil Bay, 1867 (fl), *Moquerys 66* (G, Z); Reserve no. 1, Tamatave, 21 June 1950 (fl), *Rakotoniama sub RN 3956* (MAD, 2 sheets); Sainte Marie Island (East Coast), Sept. 1851 (fl), *Boivin s.n.* (P, syntype); (fl), *Boivin s.n.* (P, syntype); Mar. 1847 (fr), *Boivin 1728* (P, holotype of *T. boivinii*); Ambila, Lemaitsoa, littoral forest, Aug. 1975 (fl, fr), *Rakotozafy 1293* (MAD); Androndramanika, Rahobevava, 830 m (near Lac Alaoatra), 10 May 1951 (fr), *Cours sub Herb. Alaotra 4270* (MAD). WITHOUT PRECISE LOCALITY: Central Madagascar, 1883 (fl), *Baron 2499* (K); (fl), *Baron 2504* (K); Dec. 1883 (fl), *Baron 2766* (K, 2 sheets); East Coast, Mar. 1891 (fr), *Baron 6043* (K); 1865 (fl), *Gerrard 35* (K); 1883 (fl), *Humbolt 190* (K).

Tambourissa religiosa belongs to species Group 4 and appears to be most closely allied to *T. purpurea,* another Madagascan species with structurally similar leaves and flowers. Observations on living material of *T. religiosa,* however, are required to ascertain whether or not its gynoecious flowers produce a mucilaginous "hyperstigma" as do those of *T. purpurea* (studied by Endress, 1979 and 1980b, as *T. religiosa*). Ripe fruiting receptacles of both species are smooth and reddish as opposed to those of most congeners which are pale brown and corky.

Tambourissa religiosa is distinguishable from *T. purpurea* by its floral receptacles which are more than twice as large, its more numerous stamens with separate loculi and distinct filaments, its more numerous, acute styles, and by its larger, more coriaceous leaves with a thicker hypodermis, prominent partial marginal fimbrial vein, and revolute margins.

Vernacular names. Ambora, Laingafora (Madagascar). According to Commerson, certain Malagasy tribes used *Tambourissa religiosa* in a religious context, burying their dead with its branches.

22. Tambourissa purpurea (Tul.) A.DC., Prodr. 16(2): 659. 1868; Perk. & Gilg, Pflanzenr. 4, 101: 69, fig. 18:5. 1901; Perk., Pflanzenr. 4, 101 (Nachtr.): 42. 1911; Cavaco in Humbert, Fl. Madagascar 80: 39, fig. V:1. 1959.
Ambora purpurea Tul., Ann. Sci. Nat. (Paris) 4(3): 30. 1855; Tul., Monogr. Monim. 301, pl. XXVI. 1855. TYPE: Madagascar. Tamatave: Sainte Marie Island (ca. 1850) (fl, fr), *Bernier 262* (lectotype, P, here designated; isolectotype, P).

Tambourissa rota Baker, J. Linn. Soc., Bot. 20(128): 240. 1883; Perk. & Gilg, Pflanzenr. 4, 101: 70. 1901; Perk., Pflanzenr. 4, 101 (Nachtr.): 42. 1911; Perk., Gatt. Monim. fig. 34:5. 1925; Cavaco in Humbert, Fl. Madagascar 80: 38, fig. X:6. 1959. TYPE: Madagascar. Central Madagascar: without precise locality (ca. 1881) (fl, fr), *Baron 764* (lectotype, K, here designated; isolectotype, P).

T. quadrifida sensu Drake in Grandidier, Hist. Phys. Madagascar 1(1): 21. 1902, pro parte, non Sonn.

T. rota var. *longipetiolata* Perk., Pflanzenr. 4, 101 (Nachtr.): 42. 1911. TYPE: Madagascar. Central Madagascar: without precise locality (fr), *Baron 1642* (holotype, K).

Monoecious shrub, treelet, or small tree attaining 10 m tall and 30–40 cm D.B.H., the bark gray-black, longitudinally fissured, the branches often decumbent and trailing, the new growth glabrous or with rare, scattered hairs, the mature leafy stems brownish, 2–3 mm diam., terete. Leaves opposite to subopposite, rarely ternate on vigorous sucker shoots, glabrous, petiolate; petioles 3–10(–17) mm by 0.8–1.3 mm, red to purple when living; lamina chartaceous to subcoriaceous, ovate-elliptic, elliptic, oblong, narrowly oblong or obovate, (25–)40–85(–100) mm by (10–)15–40(–44) mm, the apex acuminate, acute, obtuse or retuse, the base cuneate, acute, obtuse, truncate or even subcordate, often ± decurrent, the secondary veins 4–11 pairs, making a 60–70° angle with the costa, the venation visible to 2–4° or obscure adaxially, visible to 2–3° abaxially, the margin plane to slightly revolute. Inflorescence ramiflorous, axillary, or terminal on leafy shoots, a 3-flowered dichasium or a contracted pleiochasium of 5 flowers (the gynoecious flower terminal, if present), or the flowers solitary, or in sparse fascicles on old stems, the floral axis

1–4 mm by 1 mm, glabrous to puberulent, the axis and pedicels subtended by 1 to several ciliate to hirsute, naviculate bracteoles. Androecious flower in bud sparsely pubescent to glabrous, globose-depressed to napiform-depressed, 2–3(–4) mm diam. by 2.5–3.5(–4) mm long, the apex with 1–3 pairs of minute, acute to rounded ciliate tepals, the pedicel 2.5–6(–10) mm by 0.6–1 mm; at anthesis 2.5–3.5 mm diam., shallowly (3–)4-fid for up to ½ its length, the lobes incurved or spreading slightly, the orifice 1–3 mm diam.; stamens 20–32, acutely deltoid to obtusely deltoid, 0.7–1.2 mm long by 0.6–1 mm wide, the loculi confluent apically into a single, crescentiform loculus, the filament very short or sessile, the internal receptacle surface glabrous or with rare, scattered hairs. Gynoecious flower in bud globose-depressed to napiform-depressed, glabrous to sparsely pubescent, apiculate with 2–3 pairs of minute tepals, the pedicel 5–6 mm by 1 mm; at anthesis urceolate-globose to urceolate-napiform, 4(–7) mm diam. by 4(–7) mm long, the orifice 3–4-lobed, 0.5–1 mm diam., when living occluded by a mucilaginous plug, the inner tepals stigmatic; styles 35–70(–90), shortly columnar, apiculate, 0.3–0.4 mm long by 0.2–0.3 mm diam., the internal receptacle surface glabrous or with rare, scattered hairs between the styles. Fruiting receptacle terminal, solitary, globose-urceolate, ± depressed, 28–50 mm diam. by 25–40 mm long, the external surface dark reddish brown to blackish, occasionally mottled with pale gray-brown, corky patches, the orifice subentire, ± circular, 2–7 mm diam., comprising $\frac{1}{10}$–$\frac{1}{6}$ total width of the receptacle, the walls 8–11 mm thick, the internal surface with scattered, subcircular styles ca. 0.5 mm diam., glabrous or with rare, scattered hairs. Mature carpels ovoid-compressed, 6–9 mm long, 4–7 mm wide, 3.5–5 mm thick, the endocarp brown, the surface scrobiculate to reticulate-foveate. Gametic chromosome number, $n = 19$.

Distribution. Endemic to Madagascar (Fig. 37).

Habitat. *Tambourissa purpurea* is one of the most widely distributed members of the genus in Madagascar, along with *T. hildebrandtii* and *T. religiosa*. Quite variable vegetatively, it displays a wide ecological amplitude ranging from littoral forest along the east coast, through the lowland and submontane wet forest zones of the eastern escarpment (up to ca. 1,400 m), and into montane forest of the central plateau (ca. 1,400–1,600 m). It also extends westward into the semi-deciduous dry forest zone of the western sector as far as the Isalo massif, where it is apparently able to survive annual burning, taking on a shrubby habit with numerous erect coppice shoots.

In living plants, floral receptacles of *Tambourissa purpurea* range from green to dark reddish purple. The gynoecious flowers produce a mucilaginous plug or "hyperstigma" (see Endress, 1979, 1980b) that is probably functional in pollination. Androecious flowers of *Lorence 1725* (MO) produced a faint sweet, almost musky, odor.

MADAGASCAR. FIANARANTSOA: Isalo, 13 Apr. 1961 (fl), *Anon. sub Herb. Peltier 3044* (MAD); Ihosy, Mont Lalandro, 1,100–1,200 m, 5 Nov. 1967 (fr), *Bernardi 11230* (K); Route no. 7, 39 km N of Ambositra, 1,250–1,350 m, 24 Jan. 1975 (fr), *Croat 29458* (MAD, MO); 10 km W of Ivato on Route 35, 1,365 m, 25 Jan. 1975 (fr), *Croat 29545* (MAD, MO); Massif d'Isalo, 10 km W of Ranohira, Route 7, 810 m, 3 Feb. 1975 (fl), *Croat 30568* (MAD, MO); Ambohimitombo forest (Fanala), 1,350–1,440 m, 4 Jan. 1895 (fl), *Forsyth Major 328* (K); (fl), *Forsyth Major 340* (K); 21 Jan. 1895 (fr), *Forsyth Major 710* (K); Betsileo Land, 1880 (fr), *Langley Kitching s.n.* (K); National Route no. 7 at 11 km W of Ambalavao, 950 m, 5 Nov. 1978 (fl), *Lorence 2042b* (K, MAD, MAU, MO, P, Z); (fl), *Lorence 2044* (K, MAD, MO, Z); National Route no. 7 at 9 km SW of Ranohira (Isalo), 800 m, 6 Nov. 1978 (fr), *Lorence 2058* (MAD, MO); (fr), *Lorence 2059* (MAD, MO); (st), *Lorence 2060* (MAD, MO). MAJUNGA: Natural Reserve no. 4, Marovato, Ambanja, 10 July 1952 (fr), *Safy sub RN 4180* (MAD, 2 sheets). TAMATAVE: Soanierana, Ivongo (near Sainte Marie Island), 27 Dec. 1949 (fr), *Anon. sub SF 2346* (MAD); Anjahana, Foule Pointe, 12 June 1950 (fr), *Anon. sub SF 2585* (MAD); Natural Reserve no. 3, Sahatavy, Fenoarive, 17 June 1952 (fl), *Anon. sub RN 4137* (MAD); Vohimaranitra, Tamatave, 26 Jan. 1951 (fr), *Anon. sub RN 1989* (MAD); Sainte Marie Island, Tafondron Forest, Mar. 1847 (fl, fr), *Boivin 1729* (P, syntype, 2 sheets); Morarano, pseudosteppes on dry slopes (W of Lac Alaotra), Dec. 1954 (fl), *Bosser 7502* (MAD); on sand between Mahanoro and Vatomandry, 2 July 1972 (fr), *Cremers 2310* (MAD, 2 sheets); Ambila, littoral forest, 8 May 1928 (fr), *Decary 6450* (P); Fenoarivo, 18 Mar. 1930 (fl), *Decary 7633* (MAD); National Route no. 2 at 89 km E of Tananarive, Mandraka Forest, 1,400 m, 30 Oct. 1978 (st), *Lorence 2036* (MAD, MO); Perinet, 70 km E of Tananarive (cultivated in Heidelberg Bot. Garden) Oct. 1976 (fl), *Rauh M 138* (Z). TANANARIVE: Analabe, Anjozorobe, Mar. 1953 (fr), *Bosser 5219* (MAD, 2 sheets); Tampoketsa, Ankazobe, Pk 120, road to Majunga, Apr. 1955 (fr), *Bosser 7855* (MAD); Andramasina, Ambatolampy (fl, fr), *Bosser 12466* (MAD, 2 sheets); forest at Pk 142 along the road from Tananarive to Majunga, 8 July 1971 (fr), *Cremers 1641* (MAD); Tananarive, Tsimbazaza Park, 1,200 m, 17 Jan. 1975

(fl), *Croat 28636* (MAD, MO); near Tananarive, 28 July 1928 (fr), *Decary 6610* (MAD); Tananarive, Tsimbazaza Park, cultivated in back of Philippe Morat's house (originally from Perinet), 28 May 1974, *Gentry & Morat 11964* (MAD, MO); forests of Tampoketsa, May 1956 (fr), *Rialinansy 1027* (MAD); bottom of the valley Ambohimanga south, 9 Nov. 1963 (st), *Rakotozafy 204* (MAD); "tapias" (*Uapaca* forest), Pk 36, road to Antsirabe, 16 Feb. 1966 (fl), *Rakotozafy 460* (MAD); Vakinankaratra, Ambatolampy, banks of the Onive River, near Tsinjoarivo, 1,600 m, 1 Dec. 1912 (fr), *Viguier & Humbert 1913* (G). TULEAR: along road through mountain forest in Chaines Anosyennes from Fort Dauphin to Ranamafona, 40–60 m, 1–28 km from Route no. 10, 19 Feb. 1975 (fr), *Croat 31778* (MAD, MO); (fr), *Croat 31779* (MAD, MO); dunes, Fort Dauphin (fr), *Pernet sub Herb. Inst. Sci. Madagascar 29* (MAD); Fort Dauphin (fl), *Rauh 1440* (MAD). PROVINCE UNCERTAIN: Amtranokofa, Natural Reserve, 8 July 1950 (fr), *Anon. sub SF 43* (MAD); forest N of the road to Nickaville, 29 Dec. 1944 (st), *Anon. sub Herb. Alaotra 2081* (MAD); Antsahabe to Antsakalalina, 20–40 m, 5 Apr. 1949 (fr), *Anon. sub Herb. Alaotra 3607* (MAD); Andrangoalaka, Central Madagascar, 1881 (fr), *Baron s.n.* (K); 1882 (fl), *Baron 1239* (K, syntype of *T. rota*); (st), *Parker s.n.* (K); Central Majakotompo, Nov. 1955 (fr), *Bosser 8709* (MAD); Antongona, rocks, Jan. 1960 (fl), *Bosser 13509* (MAD); Pk 44, road to Majunga, Mar. 1963 (fr), *Bosser 17192* (MAD); valley of the Saonjo, May 1964 (fr), *Morat 1140* (MAD); Antongona, 16 Jan. 1960 (fl), *Peltier 1763* (MAD); Maroamalona, Rankafina, 14 Nov. 1963 (fr), *Rakotozafy 228* (MAD); Tsaravinany, Apr. 1966 (fr), *Rakotozafy 588* (MAD). WITHOUT PRECISE LOCALITY: 1881 (fl, fr), *Baron 790* (K, P, syntypes of *T. rota*); 1882 (fl), *Baron 1361* (K, P, syntypes of *T. rota*); (fr), *Baron 2996* (K); 1883 (fr), *Baron 3024* (K, P); 1885 (fr), *Baron 3515* (K, P); (st), *Baron 3575* (BM); (fr), *Baron 4241* (K, P); (fr), *Baron 4325* (K); 1892 (st), *Baron 6675* (BM); (st), *Parker s.n.* (K); North Madagascar, 1892 (fr), *Baron 6439* (K). CULTIVATED: Missouri Botanical Garden, grown from wild seed obtained from Madagascar, 23 June 1977 (fl), *Lorence 1725* (MO); (fl), *Lorence 1726* (MO); 13 Feb. 1980 (fl), *Lorence 2954* (MO).

Although *Tambourissa purpurea* is extremely variable in terms of foliar morphology, even on a single individual (e.g., *Croat 29458,* MO), its flowers are quite constant and the smallest in the genus. Along with *T. gracilis* and *T. religiosa,* it belongs to species Group 4. Flowers of *T. religiosa,* however, are about twice as large as those of *T. purpurea,* have more numerous parts, and the leaves are thicker with a well-developed hypodermis of (3–)5–6 cell layers comprising ca. ⅓–½ of the total laminar thickness. That of *T. purpurea* is only (1–)2–3 cell layers thick and comprises only ⅙–⅓ of the total laminar thickness. Also, *T. purpurea* lacks the prominent partial marginal fimbrial vein of the former species. Both occur sympatrically in eastern and central Madagascar and no hybrids or intermediates are known to occur.

Tambourissa purpurea is perhaps even more closely allied to *T. gracilis* in terms of foliar and androecious floral morphology (gynoecious flowers are unknown in the latter). The pleiochasia are much laxer in *T. gracilis,* however, with a much longer floral axis and pedicels.

Vernacular names. Ambora, Ambora vavy, Rota, Villainque-possa (Madagascar).

23. Tambourissa gracilis Perk., Pflanzenr. 4, 101 (Nachtr.): 43. 1911; Cavaco in Humbert, Fl. Madagascar 80: 35. 1959. TYPE: "Central Madagascar." Without precise locality (probably Tananarive or Fianarantsoa): ca. 1888 (fl), *Baron 2885* (holotype, K; isotype, P).

T. leptophylla sensu Drake in Grandidier, Hist. Phys. Madagascar 1(1): 23. 1902 non (Tul.) A.DC.

Dioecious (?) treelet or small tree 8–10 m, the mature leafy stems glabrous, 1.5–2.5 mm diam. Leaves opposite, glabrous, petiolate; petioles 14–17 mm by 1 mm; lamina chartaceous, elliptic or rarely oblong, 75–120 mm by 26–45 mm, the apex long acuminate, the base acutely cuneate, decurrent, the secondary veins 6–9 pairs, making a 65–85° angle with the costa, the venation raised and visible to 4° on both surfaces, the margin plane to slightly revolute. Androecious inflorescence ramiflorous on leafless nodes or axillary, a unisexual pleiochasium of 3–7 flowers, sparsely pubescent with pale, appressed hairs, the floral axis 7–25 mm by 1 mm, subtended by several basal bracteoles. Androecious flower in bud globose, 6–8 mm diam., apiculate with a pair of semicircular, obtuse tepals, the pedicel 5–13 mm by 1 mm, subtended by 1(–2) hirsute, naviculate bracteoles 1–2 mm long; at (full?) anthesis globose, 6–8 mm diam., the subcircular orifice 1–2 mm diam., occasionally splitting slightly, flanked internally by several pairs of obtuse, scale-like tepals; stamens ca. 50, broadly deltoid, 1.2–1.7 mm long by 1 mm wide, the loculi occupying almost entire length of the stamen, confluent apically into a single, crescentiform loculus, the filament very short or sessile, the internal receptacle surface with rare, scattered hairs. Gynoecious inflorescence unknown. Submature fruiting receptacles borne in clusters of 2–3, shallowly cupuliform, 30–55 mm wide by 20–30 mm long, the orifice comprising ⅔–¾ total width of

fruit, the styles conical, 0.6–0.8 mm long; fruiting carpels ovoid-compressed, 9–10 mm long by 7–8 mm wide, tan.

Distribution. Endemic to Madagascar (Fig. 37).

Habitat. According to Humbert (1965) and Cavaco (1959), *Tambourissa gracilis* occurs in high altitude ericoid heath formation (ca. 1,800–2,700 m) on mountains of the central plateau and vicinity. However, a fruiting specimen (*Humbert 3688*, P) named by him and cited by Cavaco (1959) is closer to *T. purpurea*, from which it differs in having disorganized venation characteristic of neither species. As the specimen lacks flowers, a more complete analysis is impossible.

MADAGASCAR. DIEGO SUAREZ: Tsaratanana Massif, 1,400 m, Nov. 1912 (fr), *Perrier de la Bâthie 10105* (P).

Tambourissa gracilis belongs to species Group 4. With respect to its androecious flowers, which have short, subsessile stamens and apically confluent loculi, it appears to be most closely related to *T. purpurea* which differs in having a shorter floral axis and pedicels. Foliar morphology of the two species is virtually identical, also resembling that of *T. madagascariensis* (Group 2A). Further collections of this imperfectly known species, especially gynoecious flowers and fruits, are needed to better understand its affinities.

24. Tambourissa pedicellata Baker, Fl. Mauritius 289. 1877; Perk., Pflanzenr. 4, 101 (Nachtr.): 42. 1911; Vaughan, Mauritius Inst. Bull. 1(1): 76. 1937. TYPE: Mauritius. Without precise locality; in the shade of humid forests, on the high mountains, 1864 (fl, fr), *Bouton s.n.* (lectotype, K).

Ambora amplifolia sensu Tul., Monogr. Monim. 299. 1855, pro parte, non Boj. ex Tul.

Tambourissa amplifolia sensu A.DC., Prodr. 16(2): 659. 1868, pro parte; Perk. & Gilg, Pflanzenr. 4, 101: 70. 1901, pro parte, non (Boj. ex Tul.) A.DC.

Monoecious tree attaining 15 m tall and 30 cm D.B.H., the crown compact, the bark pale brown, smooth, flaking, the new growth sparsely puberulent, glabrescent, the mature leafy stems 2.5–6 mm diam., terete, the nodes dialated. Leaves opposite, rarely subopposite, glabrous, petiolate; petioles (2–)6–13 mm by 1.5–3 mm; lamina chartaceous to coriaceous, elliptic to narrowly elliptic or oblong, rarely broadly elliptic to suborbiculate, (30–)50–160(–200) mm by (15–)22–80(–120) mm, the apex acuminate, acute, obtuse, rounded or retuse, the base acutely decurrent to acutely cuneate, the secondary veins 5–12 pairs, making a 50–65° angle with the costa, the venation obscure adaxially and visible to 2(–3°), dark brown abaxially and visible to 3(–4°), the margin slightly thickened, moderately revolute. Inflorescence a glabrous, ramiflorous (rarely terminal), leafless or leafy, unisexual or sexually mixed pleiochasium of 5–14 flowers, or a cauliflorous, leafy or leafless pleiochasium or rarely dichasium, the floral axis (15–)35–200 mm by 1.5–4 mm, often ± flattened, frequently subtended by several deltoid-naviculate puberulent bracteoles; flowers monomorphic. Androecious flower in bud napiform-depressed, 7–11 mm diam. by 4–7 mm long, externally smooth with scattered hairs, the apex with 4 minute, puberulent tepals, the pedicel long, slender, 15–66 mm by 0.7–1.5 mm, subtended by a single puberulent, subulate-deltoid bracteole 1–2 mm long or by a small leaf; at anthesis shallowly 4–6-fid, subglobose, 10–14 mm diam., the lobes thick, short, acuminate, incurved to erect, the orifice comprising ½–⅔ total width of the receptacle; stamens 50–70, minute, deltoid to ellipsoid, 0.6–1 mm long by 0.5–0.8 mm wide, the loculi short, broad, subparallel, separate or occasionally confluent apically, sometimes ± unilateral, occupying ⅔–¾ total length of the stamen, the filament short, basally ventricose, the connective not prolonged, the internal receptacle surface glabrous. Gynoecious flower in bud subglobose to napiform-depressed, 8–10 mm diam. by 5–7 mm long, externally smooth with scattered hairs, the apex with 3–4 minute, puberulent tepals, the pedicel as in the androecious flower; at anthesis shallowly 4–7-fid, subglobose, 6–12 mm diam. by 5–7 mm long, the lobes thick, acute to acuminate, erect, the orifice subentire, comprising ca. ½–⅔ total width of the receptacle, the walls thick; styles ca. 60–180, conical, 0.8–1.2 mm long by 0.3–0.4 mm wide basally, the apex slightly papillose, the base ventricose, the internal receptacle surface glabrous or with sparse clusters of hairs between the styles. Fruiting receptacle produced on the branches, solitary or in a leafy pleiochasium of up to 5 fruits, ± subglobose, 18–32 mm diam. by 12–25 mm long, the orifice small, shallow, comprising ca. ¼–½ total width of the receptacle, the rim subentire, thickened, with persistent deltoid lobes, the external surface mottled, pale corky brown with darker patches,

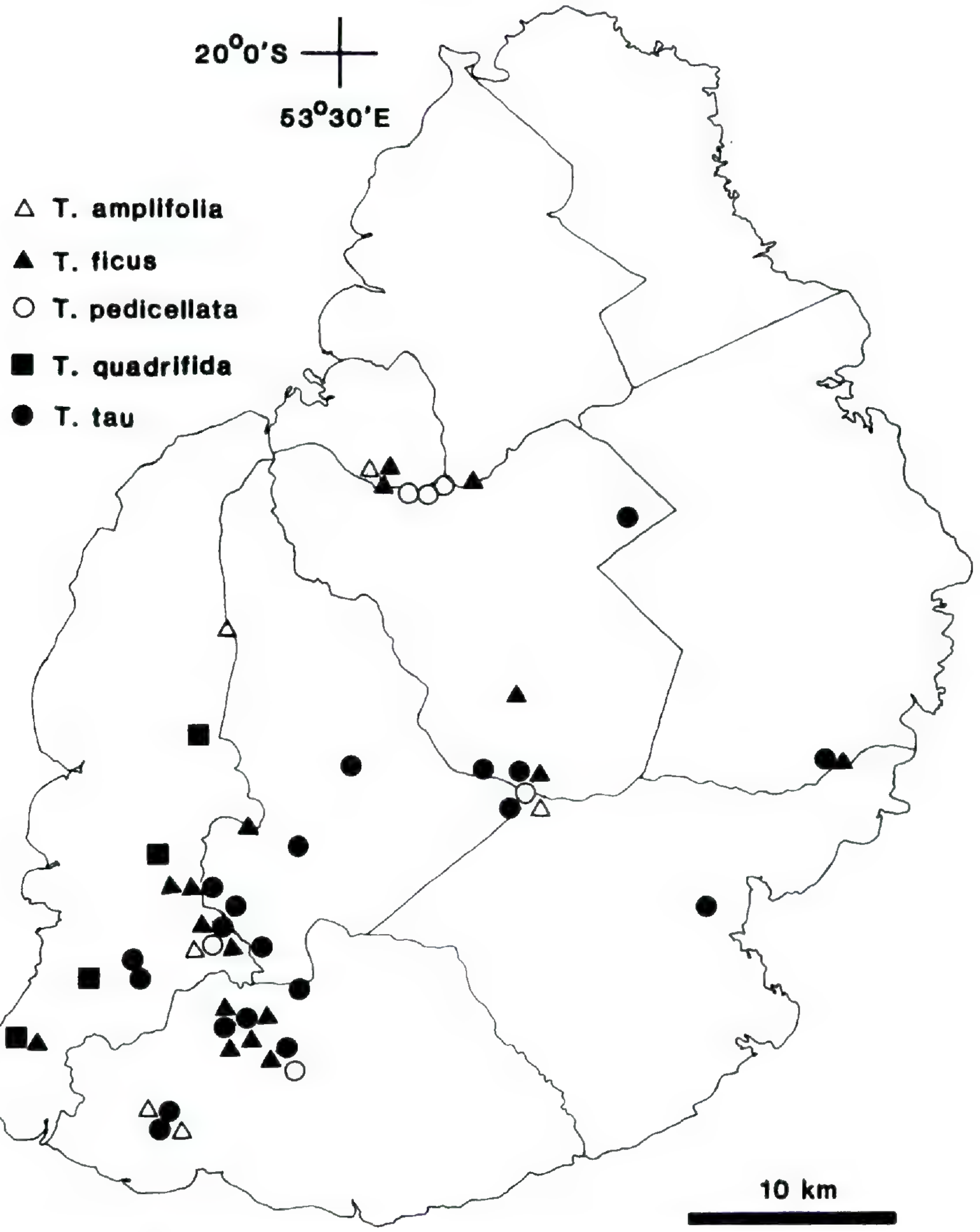


FIGURE 38. Distribution map of some *Tambourissa* species in Mauritius.

the cavity small, the numerous styles conical, 0.6–1 mm long by 0.4–0.7 mm diam. basally, interspersed with rare, scattered hairs, the pedicel slender, 20–55 mm by 1.5–2.5 mm. Mature carpels ovoid-compressed, 8–11 mm long, 6–8 mm wide, 4–6 mm thick, the endocarp dark brown with 1 to several longitudinal, ± branching ridges, the surface foveate-scrobiculate. Gametic chromosome number, $n = 19$.

Distribution. The species is endemic to Mauritius (Fig. 38).

Habitat. Tambourissa pedicellata is presently known only from four localities in wet and cloud forest: the southern flank of the Pieter Both mountain range, where I estimate the total population to consist of 50 to 100 individuals; at Mt. Lagrave, where a small population occurs in cloud forest near the summit; in Bassin Blanc crater, where a single individual was located. Vaughan and Wiehe (1941) recorded *T. pedicellata* from Macabé forest (*Vaughan 1327 sub MAU 2358*, MAU), but I was unable to relocate it there during extensive searches made in 1974–1977 and again in 1978–1979. In 1983, W. Strahm (pers. comm.) located an "individual" of *T. pedicellata* at Macabé whose trunk was fused with that of *T. sieberi* in what apparently represents a perfect natural graft.

My observations on the Pieter Both population during the course of a year showed the plants to be evergreen and not deciduous as stated by Vaughan and Wiehe (1941). Most individuals

here flowered from February through April 1979, although one tree was flowering in November 1978. Fruits generally ripened in February. Living flowers of *T. pedicellata* produce little apparent odor, although a faint, fruity smell was detected in some. Buds and receptacles are mottled green externally, and the stamens may be cream, yellow, or yellowish pink, whereas the styles range from bright orange to reddish orange.

MAURITIUS. BASSIN BLANC CRATER: wet forest near lake, ca. 500 m, 6 July 1979 (st), *Lorence 2967* (MO). MACABÉ FOREST: Macabé transect (symbol T_2) 16 June 1937 (st), *Vaughan 1327 sub MAU 2358* (MAU). MT. LAGRAVE: S slope facing Eau Bleue reservoir, near summit, ca. 600–628 m, 24 May 1979 (st), *Lorence 2966* (MO). PIETER BOTH MOUNTAIN RANGE: S flank, 500–600 m, 29 Nov. 1978 (fl), *Lorence 1834* (K, MAU, MO, 2 sheets; P); 13 Feb. 1979 (fl), *Lorence 2384* (K, MAU, MO, 2 sheets; Z); (fl, fr), *Lorence 2385* (B, G, K, MAU, MO); (fl, fr), *Lorence 2386* (K, MAU, MO, P, REU); 19 Apr. 1979 (fl), *Lorence 2598* (MAU, MO); (fl), *Lorence 2599* (MAU, MO). QUARTIERE MILITAIRE: 1863 (fl), *Anon. sub Herb. Blackburn s.n.* (K, syntype, 2 sheets). WITHOUT PRECISE LOCALITY: (fl, fr), *Anon. sub Herb. Richard s.n.* (P); (fl), *Anon. sub MAU 1311* (MAU); 1814 (fl, fr), *Carmichael s.n.* (K); ca. 1755 (fl), *Commerson s.n.* (P); (st), *Anon. sub Herb. Ventenat s.n.* (G, 2 sheets).

In terms of floral morphology, *Tambourissa pedicellata* appears to be one of the least specialized species in Mauritius and possibly in the entire genus. It appears to fit best in species Group 5, however. Among Mauritian species, *T. pedicellata* is most similar to *T. amplifolia* which also has long, slender floral pedicels, small subglobose buds and receptacles, and small stamens and styles; the two species have been confused in the past (De Candolle, 1868; Perkins & Gilg, 1901). *Tambourissa amplifolia* is readily distinguishable, however, by its smaller, more slender habit, basal cauliflory, much larger leaves, discoid gynoecious flowers with everted lobes, and androecious flowers deeply split into four flat lobes bearing stamens with apically confluent loculi.

Although *Tambourissa purpurea* (Madagascar) also has monomorphic androecious and gynoecious flowers, it appears to represent a highly specialized condition because of the mucilaginous "hyperstigma" of the gynoecious flowers (see Endress, 1979, 1980b; as *T. religiosa*). The majority of Mauritian species with opposite leaves, more or less open, cupuliform to napiform or globose gynoecious flowers and conical to setose styles also belonging to Group 5 may have been derived from a common ancestor which *T. pedicellata* most closely approaches today.

25. Tambourissa amplifolia (Bojer ex Tul.) A.DC., Prodr. 16(2): 659. 1868; Baker, Fl. Mauritius 287. 1877; Perk. & Gilg, Pflanzenr. 4, 101: 70. 1901, pro parte; Perk., Pflanzenr. 4, 101 (Nachtr.): 43. 1911. *Mithridatea amplifolia* Bojer, Hortus Maurit. 290. 1837 nom. nud. *Ambora amplifolia* Bojer ex Tul., Monogr. Monim. 299. 1855. TYPE: Mauritius. Woods of Grand Port: Pouce Mountain, Aug. 1851, *Boivin s.n.* (holotype, P).

Monoecious understory treelet or small tree attaining 8 m tall and 9 cm D.B.H., sometimes shrubby, the branches few, erect, the new growth sparsely hirsutulous, the leafy stems terete, 5–14 mm diam., glabrous, the nodes dialated. Leaves often clustered near the ends of the branches, opposite to subopposite, sometimes congested into pseudoverticels of 4, glabrous, petiolate; petioles 14–30 mm by 4–8 mm; lamina chartaceous to subcoriaceous, elliptic to ovate or narrowly ovate, sometimes ± falcate, 150–450(–500) mm by 80–230(–240) mm, the apex acute to acuminate, the base obtusely decurrent to obtusely cuneate or acutely cuneate to acutely decurrent, the secondary veins 7–9 pairs, making a 60–70° angle with the costa, the venation raised and prominent, visible to 4–5° on both surfaces, the margin plane to slightly revolute; seedling and sucker leaves heterophyllous, with 1–3 pairs of serrate teeth in the apical portion, the petiole red when living. Inflorescence basally cauliflorous (exceptionally ramiflorous), on meristematic swellings up to ca. 1 m above ground level, the flowers solitary, fasciculate or in a unisexual or sexually mixed pleiochasium of 3–7, the gynoecious flower often terminal, the floral axis 5–20(–45) mm by 1.2–2 mm, finely pubescent, basally bracteolate. Androecious flower in bud globose, puberulent, 7–8 mm diam., apiculate with 4 minute tepals, the pedicel 25–60 mm by 0.8–1 mm, pubescent, subtended by a minute, caducous deltoid bracteole; at anthesis deeply 4-fid, 14–18 mm diam., the lobes thick, spreading almost flat or slightly incurved, the internal receptacle surface glabrous; stamens numerous, ca. 100–250, obovoid to clavate, 0.8–1.5 mm long by 0.5–0.6 mm wide, the loculi confluent at the obtuse apex (very rarely separate), occupying the apical ½–⅔ of the stamen, the connective not

prolonged, the filament distinct, slender. Gynoecious flower in bud napiform-discoid, pubescent, the apex depressed, with an apicule or several pairs of minute tepals, the pubescent pedicel 38–80 mm by 1.5 mm; at anthesis shallowly napiform-discoid, 11–13 wide by 4–6 mm long, the apex splitting into 4(–6) everted deltoid lobes, the orifice ± square or subcircular, comprising ca. ½ total width of the receptacle; styles numerous, ca. 300, shortly conical, 0.6–1 mm long by 0.2–0.3 mm wide basally, the internal receptacle surface velutinous with dense, simple hairs between the styles. Fruiting receptacle solitary at the base of the trunk (exceptionally on the branches), napiform-urceolate or subglobose, 30–56 mm diam. by 22–45 mm long, the orifice ca. 25 mm diam., comprising ca. ½ total width of the receptacle, subentire, bearing remnants of the indurated lobes, the walls ca. 12 mm thick, the external surface corky brown, bumpy, with several prominent veins, the internal surface with numerous shortly conical styles 0.6–1 mm long by 0.2–0.3 mm wide basally, interspersed with scattered simple hairs, the pedicel and peduncle (15–)35–80 mm by 4–5 mm. Mature carpels ovoid-compressed, 12–13 mm long, 6–8 mm wide, 4–5 mm thick, the endocarp light brown, with an irregular network of low ridges, the surface slightly foveate-scrobiculate.

Distribution. Endemic to Mauritius (Fig. 38).

Habitat. *Tambourissa amplifolia* is local and occasional to common in the lower montane wet forest zone at Bel Ombre (200–400 m), at Plateau Colophane below Macabé Forest (ca. 500 m), on the summit of Mt. Corps de Garde (ca. 750 m), in cloud forest on Mt. Lagrave (500–628 m), and in moist forest on the crest of Piton du Fouge (650 m).

MAURITIUS. BEL OMBRE FOREST: Bel Ombre Nature Reserve, 7 Dec. 1971 (fl), *Guého sub MAU 15195* (K, 2 sheets; MAU); 200–400 m, 27 Dec. 1978 (st), *Lorence 2216* (MO); (st), *Lorence 2217* (MO); (st), *Lorence 2218* (MO); (fl), *Lorence 2219* (MO, Z); (fl), *Lorence 2220* (MO, P); (fl), *Lorence 2221* (K, MO); (fl), *Lorence 2222* (K, MAU, MO, REU); (fl), *Lorence 2223* (MO, P); 10 Jan. 1979 (fl), *Lorence 2259* (MAU, MO); 16 Feb. 1979 (fl), *Lorence 2408* (MO); 3 July 1979 (st), *Lorence 2691* (MO, 2 sheets); (fr), *Lorence 2692* (MO). CORPS DE GARDE MT.: summit ridge, ± stunted forest, 15 Nov. 1973 (fl), *Coode et al. 4066* (K, MAU); 8 Nov. 1971 (fl), *Guého sub MAU 14928* (MAU, 2 sheets). PITON DU FOUGE: crest of Piton du Fouge, low, dryish forest, ca. 600 m, 24 Jan. 1976 (fl), *Lorence 1629* (MAU). MACABÉ FOREST: Plateau Colophane below Macabé, ca. 600 m, 15 Jan. 1979 (st), *Lorence 2280* (MAU, MO); (st), *Lorence 2281* (MO); near Macabé, uplands, ca. 600 m (st), *Vaughan sub MAU 1510* (MAU); Macabé high forest, 660 m, May 1938 (st), *Vaughan sub MAU 1603* (MAU). MT LAGRAVE: 500–600 m, 19 Feb. 1979 (st), *Lorence & Lecordier 2362* (MO). WITHOUT PRECISE LOCALITY: (fl), *Anon. s.n.* (BM); 1863 (fl), *Anon. sub Herb. Blackburn s.n.* (K); (fr), *Anon. sub Herb. Brown s.n.* (K); (fl), *Anon. sub Herb. Cosson s.n.* (P, 2 sheets); 1865 (fl, fr), *Anon. sub Herb. De Candolle 16(2): 659, no. 3* (G, 3 sheets; MO, microfiche); (st), *Anon. sub Herb. Inst. Sci. Madagascar s.n.* (P); (st), *Boivin s.n.* (K, P, possibly isotypes of *T. amplifolia*); 1814 (st), *Carmichael s.n.* (K); ca. 1755 (fr), *Commerson s.n.* (P); (fl), *Commerson 67* (P, 2 sheets); (fl), *s.n. sub Herb. Juss. 16708* (P-JUSS; MO, photo); (st), *Ilardwicke s.n.* (G).

Tambourissa amplifolia belongs to species Group 5 and appears to be most closely related to *T. tau,* which differs in having relatively smaller leaves consistently aggregated into pseudoverticels of two to four pairs separated by long "internodes," by its T-shaped stamens with separate loculi, and by its long, setose styles, and internally glabrous gynoecious receptacles. Fruiting carpels of *T. amplifolia, T. pedicellata,* and *T. tau* all have endocarps with a series of low, ± branching ridges, a feature unknown in other species and perhaps suggestive of a close affinity between these species.

Bel Ombre forest harbors the largest known population of *Tambourissa amplifolia,* where it occurs sympatrically with *T. tau.* No intermediates or suspected hybrids were found here despite concurrent flowering times from December to February.

Populations that approach *Tambourissa tau,* however, occur in the eastern mountain ranges of Mt. des Créoles (*Lorence & Julien 2337,* MAU, MO) and also Piton Bambou (*Staub sub MAU 13493,* MAU). Although these plants resemble *T. amplifolia* in having large, acuminate petiolate leaves, their flowers most closely approach *T. tau* in being axillary (in *Staub sub MAU 13493*) and externally corky brown with multiple, incurved orifice lobes and long, setose styles (in *Lorence & Julien 2337*). Stamens are critical in distinguishing the two species; unfortunately, androecious flowers are absent in both collections. Another intermediate collection, without precise locality (*Anon. sub Herb. Brown s.n.,* K), approaches *T. tau* in having ramiflorous, shortly pedicellate fruits, but the shortly conical styles are characteristic of *T. amplifolia*; androecious flowers are absent also.

The holotype of *Tambourissa amplifolia,* either

from Grand Port or the Pouce Mt., possesses abnormally short floral pedicels (8–10 mm long) and almost glabrous androecious buds. Although lowland forest in the Grand Port region no longer exists, Boivin's type is similar to recent collections from the nearby Mts. Bambous and Des Créoles in some respects. The type's obovate, obtuse stamens with confluent loculi are characteristic of the species as a whole, as are the broad, petiolate leaves, so there can be no doubt as to which species it represents despite the anomalous pedicels and bud pubescence. As *T. amplifolia* and *T. tau* remain morphologically distinct over much of their range, particularly at Bel Ombre where I studied them, I have decided to regard them as distinct species.

Living flowers of *Tambourissa amplifolia* have externally yellow-green to purple-red receptacles, cream to pale orange-yellow stamens, and pale yellow-pink to dark purple styles. A vague, faintly fruity odor is produced by the flowers.

Vernacular name. Bois tambour (Mauritius).

26. Tambourissa tau Lorence, Bull. Mus. Hist. Nat. (Paris), Ser. 4, Sect. B, Adansonia 3(3): 303, pl. 3, figs. 14, 15. 1982. TYPE: Mauritius. Perrier Nature Reserve: wet forest with *Sideroxylon* dominant, 600 m, 8 Oct. 1978 (fl), *Lorence 1835* (holotype, MO; isotypes, B, K, MAU, P, Z).

Little-branched monoecious understory treelet, rarely shrubby, 1–4 m tall, the stems to 75 mm diam., the new growth sparsely puberulent or with rare, scattered hairs, the mature leafy stems glabrous, terete, 4–7 mm diam. Leaves opposite, decussate, clustered into pseudoverticels of 2–4 pairs, sessile to subsessile, rarely shortly petiolate, glabrous; petioles stout, 1–8 (–15) mm by 3–6 mm; lamina subcoriaceous to coriaceous, broadly elliptic to narrowly elliptic, obovate or oblanceolate, rarely ovate, (70–)150–300 mm by (30–)45–130 mm, the apex shortly acuminate, shortly acute, obtuse, rounded or retuse, the base subcordate, rounded, obtuse, cuneate or acutely cuneate, the secondary veins (4–)6–9 pairs, making a 50–65° angle with the costa, the venation raised, visible to 3(–4°) adaxially, visible to 4(–5°) abaxially, the margin slightly to moderately revolute; seedling leaves heterophyllous with 2–3 pairs of short, serrate teeth in the apical portion, the petioles red when living. Inflorescence cauliflorous on meristematic swellings along entire length of the stem, occasionally ramiflorous or axillary, the flowers solitary, in a fascicle or dichasium of 2–3, or rarely in a short pleiochasium of 3–6 flowers, sexually mixed or not, the floral axis 2–3(–5) mm by 1–1.5 mm, ± corky, glabrous or sparsely puberulent basally, subtended by several small, ciliate, naviculate-deltoid bracteoles. Androecious flower in bud globose, ± depressed, the apex with several minute, deltoid tepals, the external surface corky brown, mottled, the pedicel 6–20 mm by 1–1.5 mm, basally bracteolate; at anthesis 4–6-fid, 20–25 mm diam., the lobes spreading flat, the internal receptacle surface glabrous; stamens numerous, ca. 100–150, T-shaped, 1–1.5 mm long by 1.5–2 mm wide, the loculi separate on lateral arms (rarely ± sessile, but never confluent), the filament distinct, slender, the connective slightly prolonged apically or not. Gynoecious flower in bud turbinate-depressed to napiform-depressed, 7–10 mm diam. by 4–5 mm long, externally corky brown, apiculate with several minute tepals, the pedicel 6–20(–40) mm by 1–1.5 mm, subtended by several pairs of deltoid bracteoles; at anthesis napiform-urceolate, 10–12 mm diam., the orifice splitting into 5–10 thick, irregularly deltoid, straight or incurved lobes, the orifice 3–6 mm diam., comprising ca. ⅓–½ total width of receptacle; styles numerous, ca. 80–100, slender, setose, 2–3 mm long by 0.3–0.5 mm wide at the ventricose base, the internal receptacle surface glabrous. Fruiting receptacle solitary on the main stem or major branches, rarely axillary or subterminal, shallowly cupuliform-patelliform to subglobose, 25–50 mm diam. by 10–27 mm long, the orifice 10–26 mm diam., comprising ca. ½ total width of the receptacle, subentire with 5–6 indurated deltoid lobes, the walls 10–14 mm thick, the external surface corky brown, bumpy, the internal surface with numerous scattered, setose styles 1.5–3.5 mm long by 0.3–0.4 wide basally, otherwise glabrous, the pedicel stout, 8–20 mm by 2–7 mm. Mature carpels ovoid-compressed, 10–14 mm long, 6–8 mm wide, 4–6 mm thick, with occasional low, irregular ridges, the surface scrobiculate to foveate. Gametic chromosome number, $n = 19$. Figure 39.

Distribution. Endemic to Mauritius (Fig. 38).

Habitat. This is one of the commonest and most widespread members of the genus in Mauritius, occurring in most medium to upper altitude wet and cloud forest communities from ca. 300 to 800 m.

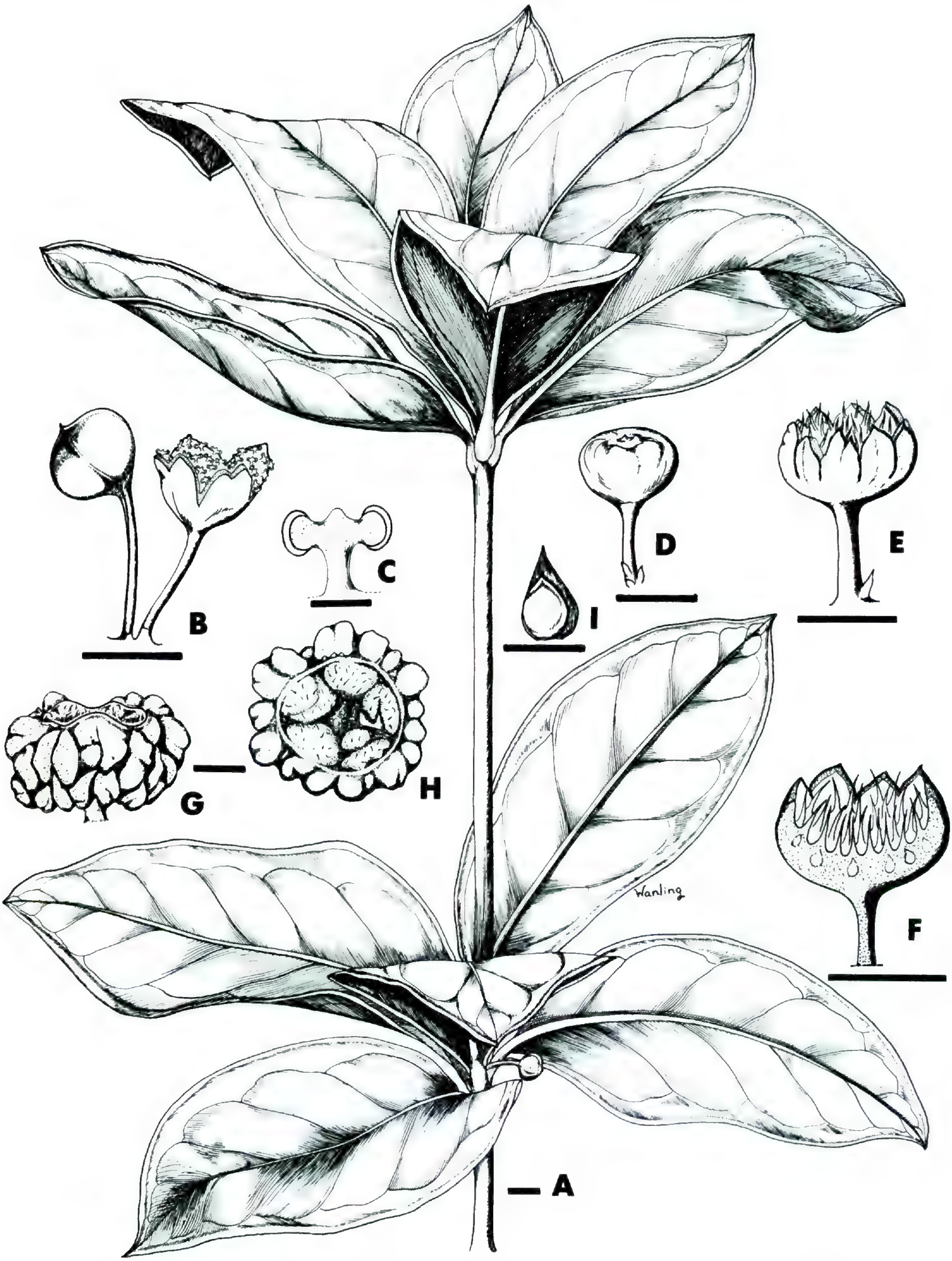


FIGURE 39. *Tambourissa tau* Lorence.—A. Habit.—B. Androecious bud and newly opened androecious flower, lateral view.—C. Stamen, lateral view.—D. Gynoecious flower in bud, lateral view.—E. Gynoecious flower at anthesis, lateral view.—F. Gynoecious flower, longitudinal section.—G. Submature fruiting receptacle, lateral view.—H. As in G, apical view.—I. Fruiting carpel, lateral view. A. Perrier Nature Reserve, Mauritius (Lorence photo, unvouchered). B–F. *Lorence 1835* (MO). G, H. *Lorence 2950* (MO). I. *Lorence 2629* (MO). Bars equal 10 mm in A, B, D–I, and 1 mm in C.

MAURITIUS. BASSIN BLANC: side of track to E side of lake, 550 m, 25 May 1976 (fr), *Richardson et al. 4163* (K). BEL OMBRE FOREST: ca. 200–400 m, 27 Dec. 1978 (fl), *Lorence 2215* (MO); 10 Jan. 1979 (fl), *Lorence 2257* (MO); (fl), *Lorence 2258* (MO). CUREPIPE BOTANICAL GARDEN: near lake, 30 June 1966 (fl), *Vaughan sub MAU 12203* (MAU, 3 sheets). GAULETTES SERRÉES: low mixed wet forest over lava, 400–450 m, 19 May 1979 (fl), *Lorence et al. 2641* (MO). GRAND BASSIN: upland thicket, 22 Sept. 1932 (st), *Orian sub MAU 47* (MAU). MACABÉ FOREST: high forest, 660 m, 18 Oct. 1978 (fl), *Lorence et al. 1863* (MO); Macabé to Brise Fer road, 660 m, 8 Dec. 1978 (fl), *Lorence 2102* (MAU, MO); (fr), *Lorence 2103* (MO); Mare Longue to Macabé road, low indigenous thicket, 1 Nov. 1962 (fl), *Vaughan sub MAU 10472* (MAU). MIDLANDS: vestige of indigenous vegetation along river, 400 m, 9 Feb. 1979 (fl), *Lorence & Lecordier 2357* (MO). MONTAGNE COCOTTE: cloud forest, 770 m, 1 Dec. 1978 (st), *Lorence 1975* (MO); (fl), *Lorence 1976* (MAU, MO); (fl), *Lorence 1977* (MAU, MO); 19 Dec. 1978 (fl), *Lorence & Lecordier 2161* (MAU, MO); (st), *Lorence & Lecordier 2165* (MO). MONTAGNE DES CRÉOLES: transitional evergreen forest, 250–300 m, 25 Jan. 1979 (fl), *Lorence & Julien 2337* (MAU, MO); (st), *Lorence & Julien s.n.* (MAU). MONTAGNE LAGRAVE: flank facing Eau Bleue reservoir, 5 Apr. 1974 (fr), *Coode et al. sub MAU 17615* (MAU); N part, summit area, degraded cloud forest invaded by exotics, 500–600 m, 9 Feb. 1979 (fl), *Lorence & Lecordier 2363* (MO); S slope facing Eau Bleue reservoir, cloud forest invaded by exotics, 600 m, 24 May 1979 (fr), *Lorence & Lecordier 2649* (MO). PERRIER NATURE RESERVE: dense indigenous thicket, 14 May 1970 (fr), *Guého sub MAU 14297* (MAU); lower montane wet forest, ca. 600 m, 8 Oct. 1978 (fl), *Lorence 1836* (MO); (fl), *Lorence 1837* (MO); 13 Oct. 1978 (st), *Lorence 1841* (MO); 12 May 1979 (fr), *Lorence 2628* (K, MAU, MO, P); (fr), *Lorence 2629* (MO); Perrier near Mare aux Vacoas, 10 Sept. 1937 (st), *Vaughan sub MAU 1404* (MAU); 25 Oct. 1962 (fl), *Vaughan sub MAU 10473* (MAU). PÉTRIN NATURE RESERVE: low *Sideroxylon* wet forest, 630 m, 12 Dec. 1978 (fl), *Lorence 2122* (MAU, MO). PITON BAMBOU: near crest of hill on the leeward side, 14 Aug. 1968 (fl), *Staub sub MAU 13493* (MAU; approaches *T. amplifolia*). PITON DE LA RIVIÈRE NOIRE: lower montane wet forest, 700–827 m, 25 Nov. 1978 (fl), *Lorence 1964* (MAU, MO); 26 Dec. 1978 (fl), *Lorence 2204* (MO). PLAINE LIEVRE: by side of road to Brise Fer, indigenous thicket, 9 Mar. 1969 (fr), *Guého sub MAU 13750* (MAU); stunted forest around clearing, 600 m, 27 Aug. 1979 (fl), *Lorence et al. 2923* (K, MO). VALLEY OF CASCADE 500 PIEDS: *Calophyllum*/Sapotaceae wet forest, 550 m, 18 May 1979 (fl), *Lorence 2634* (MO). WITHOUT PRECISE LOCALITY: (fr), *Anon. sub Herb. Richard s.n.* (P); 14 Jan. 1930 (fl, fr), *Vaughan 382* (K, 3 sheets).

Tambourissa tau is most closely allied to *T. amplifolia,* with which it has been confused in the past (e.g., Vaughan & Wiehe, 1937, 1941, in their vegetational sampling analyses at Mt. Cocotte, Macabé Forest and Perrier). Both belong to species Group 5 and have large leaves, making them difficult to separate vegetatively, although they are easily separable by floral characters. *Tambourissa amplifolia* has pubescent inflorescences, internally velutinous gynoecious flowers with shorter, non setose styles, and apically confluent anther loculi never found in *T. tau* (see *T. amplifolia* for further discussion). The specific epithet *tau* is Greek, Latin, and Celtic for "T," referring to the characteristically T-shaped stamens which are unique in the entire genus.

A plant growing in the Curepipe Botanical Garden (*Vaughan sub MAU 12203,* MAU) is typical of *Tambourissa tau* in all characters except the anomalous staminal loculi, which are sessile and not borne on extended lateral arms, although neither are they apically confluent as in *T. amplifolia.* Furthermore, gynoecious flowers of *Vaughan sub MAU 12203* are typical of *T. tau.* Flynn and Rowley (1972) studied the ultrastructural development of the pollen wall of this same plant as *T. amplifolia.*

Flower color morphs with either dark reddish purple or pale pink to greenish white stamens and styles occur; these are generally constant within a given population (e.g., dark red-purple as Perrier, pale pink or white at Mt. Cocotte). The flowers produce no apparent odor.

Vernacular name. Bois tambour (Mauritius).

27. Tambourissa tetragona (Boiv. ex Tul.) A.DC., Prodr. 16(2): 659. 1868; Baker, Fl. Mauritius 289. 1877; Perk. & Gilg, Pflanzenr. 4, 101: 70. 1901. *Ambora tetragona* Boiv. ex Tul., Ann. Sci. Nat. (Paris) 4(3): 30. 1855; Tul., Monogr. Monim. 302. 1855. TYPE: Ile de France (Mauritius). Without precise locality (ca. 1755) (st), *Commerson s.n.* (lectotype, P, here designated).

Dioecious (?), sparsely branching slender treelet or small tree attaining 6 m tall and 10 cm D.B.H., the bark pale brown, smooth with longitudinal fissures, the new growth glabrous, the mature leafy stems quadrangular, 4–6 mm diam., with 4 low wings ca. 1–1.5 mm wide. Leaves opposite, rarely subopposite, petiolate, glabrous; petioles stout, 5–15 mm by 2–3 mm, winged, the wings decurrent onto the stem; lamina subcoriaceous, narrowly obovate, oblanceolate, narrowly oblong or rarely narrowly elliptic, 52–180 mm by 17–48 mm, the apex shortly acuminate, rarely shortly acute, the tip indurated, the base acute, strongly decurrent along the petiole, the

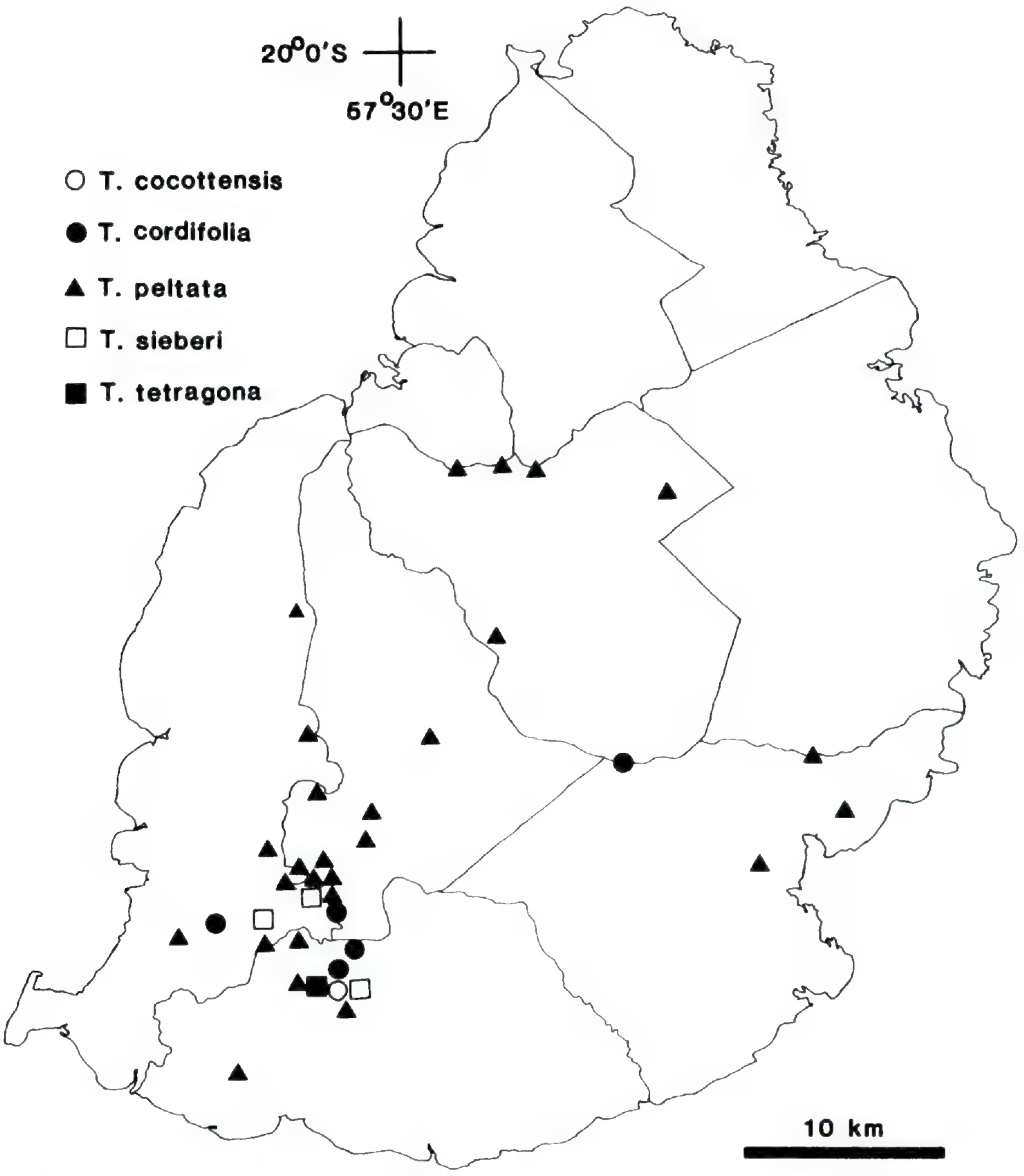


FIGURE 40. Distribution map of some *Tambourissa* species in Mauritius.

secondary veins 8–13 pairs, making a 65–80° angle with the costa, the venation obscure, visible to 2° on both surfaces, the margin revolute. Cauliflorous, the androecious inflorescence (fide Tulasne) a sparse pleiochasium, the buds globose, inaperturate, shortly pedicellate, the stamens and mature androecious flowers unknown; gynoecious inflorescence a short, glabrous, rarely leafy pleiochasium of 5–11 flowers, the floral axis quadrangular, 7–13 mm by 2–2.5 mm, subtended by several pairs of glabrous, decussate naviculate bracteoles 1 mm by 0.5 mm, the pedicel 3–4 mm by 1.5–2 mm, subtended by a glabrous, deltoid bracteole 1–2.5 mm long. Gynoecious flower in bud napiform-depressed, 8–10 mm diam. by 6–8 mm long, apiculate with 4 small, glabrous obtuse tepals, the external surface drying wrinkled, glabrous, the walls thick; at anthesis the apex splitting into 4(–5) deltoid lobes ca. 3 mm long and wide, the orifice small, ca. 1 mm wide, X-shaped, the lobes hirsute internally; styles numerous, ca. 200, shortly conical, 0.6–0.8 mm long by 0.5–0.7 mm wide at the strongly ventricose base, the internal receptacle surface glabrous between the styles. Fruiting receptacle and carpels unknown.

Distribution. Endemic to Mauritius (Fig. 40).

Habitat. *Tambourissa tetragona* is presently known only from low cloud forest on the summit of Mt. Cocotte at the southern extremity of the central plateau.

MAURITIUS. GRAND PORT: woods of the Grand Port District, Aug. 1851 (st), *Boivin s.n.* (P, syntype). MONTAGNE COCOTTE: Aug. 1977 (st), *Friedmann 3201* (P); summit, 11 Dec. 1979 (st), *Guého & Lecordier sub MAU 19501* (MAU); low, degraded cloud forest on summit, 770 m, 19 Dec. 1978 (st), *Lorence & Lecordier 2164* (MO); (st), *Lorence & Lecordier 2166* (K, MAU, MO); 17 Jan. 1979 (st), *Lorence 2286* (MO); 30 Aug. 1979 (fl), *Lorence et al. 2928* (MO); Dec. 1937 (fl), *Vaughan sub MAU 1508* (MAU); (fl), *Vaughan sub MAU 1706* (MAU). WITHOUT PRECISE LOCALITY: (st), *Anon. sub Herb. Richard s.n.* (P).

The leaves, female receptacle, and styles of *Tambourissa tetragona* are morphologically similar to those of *T. cocottensis,* a species also confined to a small patch of cloud forest on the summit of Mt. Cocotte, one of the island's highest and wettest spots. Although androecious flowers and fruiting receptacles of the former are required to further assess its affinity, both belong to species Group 5. The distinctive quadrangular, winged stems of *T. tetragona,* however, set it apart from all other members of the genus.

In the living state, leaves of *Tambourissa tetragona* have a lustrous, dark green lamina and red petiole, the stems being pale green with translucent wings. Vegetatively, it is one of the most attractive members of the genus. Gynoecious buds are shiny green flushed with dark red-purple. Buds are initiated in July and August and appear to mature in December. Known only from a single, small population in a highly degraded habitat, the species should be considered endangered. My attempts to propagate it vegetatively by cuttings failed.

Vernacular name. Bois tambour (Mauritius).

28. Tambourissa cocottensis Lorence, Bull. Mus. Hist. Nat. (Paris), Ser. 4, Sect. B, Adansonia 3(3): 295, pl. 1, fig. 2. 1982. TYPE: Mauritius. Low cloud forest, summit of Mt. Cocotte, 760 m, 19 Dec. 1978 (fl, fr), *Lorence & Lecordier 2167* (holotype, MO; isotype, MAU).

Monoecious treelet or small tree 4–5 m tall and 10–35 cm D.B.H., often multistemmed from coppices, the new growth glabrous, the mature leafy stems terete, 2–4 mm diam., longitudinally striate. Leaves opposite to subopposte, petiolate, glabrous; petioles 7–20 mm by 1–2 mm; lamina subcoriaceous, elliptic, 45–105 mm by 15–40 mm, the apex shortly acute to shortly acuminate, the tip indurated, the base acutely cuneate, slightly decurrent, the secondary veins 6–9 pairs, making a 55–65° angle with the costa, the venation visible to 3° on both surfaces, slightly raised, the margin moderately revolute. Androecious flowers solitary or in fascicles of 2, borne along the trunk. Androecious flower in bud globose, apiculate, 6 mm diam., externally corky brown, the pedicel and peduncle 4–5 mm by 1.5 mm, quadrangular, pilose, bearing 4 decussate rows of bracteoles 1 mm long; at anthesis 4–7-fid, the lobes spreading flat, 20–21 mm diam., reddish pink; stamens ca. 150–200, subsessile, linear-subulate, 3 mm by 0.6–0.8 mm, the loculi lateral, free, occupying ca. ⅔–¾ total length of stamen, the connective prolonged, slender, 1 mm long, the internal receptacle surface glabrous. Gynoecious inflorescence cauliflorous from meristematic swellings along the basal 1 m of the trunk, the flowers solitary or in fascicles of 2. Gynoecious flower in bud napiform-depressed, 9–11 mm diam. by 5–7 mm long, the apex bearing 3–4 minute, pubescent deltoid tepals, the external receptacle surface pale corky brown with scattered simple hairs, the pedicel and peduncle 4–7 mm by 1–1.5 mm, jointed near the base, quadrangular, pilose, bearing 4 decussate rows of minute, ciliate naviculate bracteoles 1–1.5 mm long; at anthesis the apex splitting into 5–7 irregular, ± inflexed deltoid lobes, the orifice comprising ca. ⅓ total width of the receptacle; styles numerous, ca. 150–200, narrowly conical, setose, 1.5–2 mm long by 0.2–0.3 mm diam. at the slightly ventricose base, the apex long acuminate, the internal receptacle surface with scattered clusters of simple hairs between the styles. Young, submature fruiting receptacle globose-urceolate, 15 mm diam. by 12 mm long, the apex depressed, the orifice subcircular, 3–4 mm diam., with 5–7 thick, deltoid lobes, comprising ca. ¼–⅕ total width of the receptacle, the external surface mottled corky brown, the internal surface with numerous setose styles 1.5–2 mm long by 0.5 mm wide basally, pilose between the styles and on the lobes, the peduncle and pedicel 5 mm by 3 mm. Mature fruiting receptacle and carpels unknown. Figure 41.

Distribution. Endemic to Mauritius (Fig. 40).

Habitat. Tambourissa cocottensis is known only from a single population on the summit of Mt. Cocotte in low cloud forest (annual precipitation 5,000 mm). Extensive searching revealed only four individuals growing within an area ca. 100 m across.

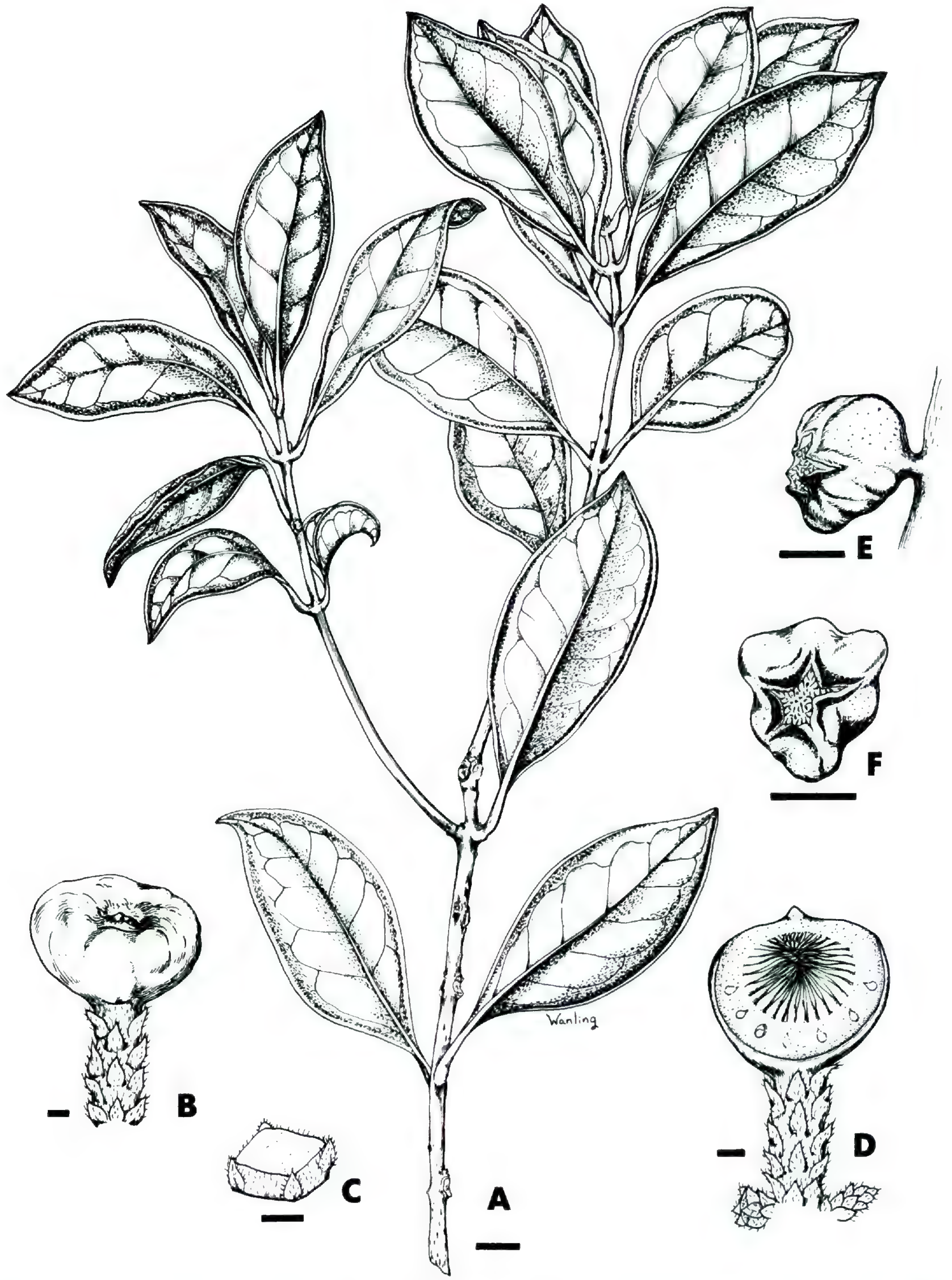


FIGURE 41. *Tambourissa cocottensis* Lorence.—A. Habit.—B. Gynoecious flower in bud, lateral view.—C. Gynoecious floral pedicel, transverse section.—D. Gynoecious flower in bud, longitudinal section.—E. Submature fruiting receptacle, lateral view.—F. As for E, apical view. A. *Lorence 2288* (MO). B–D. *Lorence 2287* (MO). E, F. *Lorence 2167* (MO). Bars equal 10 mm in A, E, F, and 1 mm in B–D.

MAURITIUS. MONTAGNE COCOTTE: summit region, low degraded cloud forest, 760 m, 17 Jan. 1979 (fr), *Lorence 2287* (K, MO, P); (st), *Lorence 2288* (MO); crest, 14 July 1982 (fl), *Lecordier sub MAU 20412* (MAU); 23 Sept. 1983 (fl), *Lecordier & Strahm sub MAU 20563* (MAU).

Tambourissa cocottensis closely resembles *T. tetragona* in a number of respects, including leaf size, shape, texture, margin, and venation, but lacks the winged stems and petioles of the latter. Both are cauliflorous with structurally similar flowers, but those of *T. cocottensis* are solitary or in fascicles of two and externally corky, differing from the smooth, glabrous pleiochasial flowers of *T. tetragona.* They more closely resemble those of *T. tau,* except for the distinctive quadrangular floral pedicels bearing four decussate rows of ciliate bracteoles. Both *T. cocottensis* and *T. tetragona* belong to species Group 5, although the prolonged staminal connectives of the latter are suggestive of certain Madagascan species.

The four known individuals of *Tambourissa cocottensis* are of different size classes, suggesting some regeneration has taken place in recent years. The two largest individuals (both gynoecious) were in bud in August 1979, and young fruits were present in December 1978 and January 1979; androecious flowers were not found. Although officially a nature reserve, the forest on Mt. Cocotte is highly degraded and has undergone extensive invasion by vigorous, weedy exotic plant species. As a result, there is a grave danger that the population is too small to maintain itself, as is also the case for *T. tetragona.* Both appear to be relictual species confined to the summit of Mt. Cocotte.

29. Tambourissa cordifolia Lorence, Bull. Mus. Hist. Nat. (Paris), Ser. 4, Sect. B, Adansonia 3(3): 296, pl. 1, figs. 5, 6. 1982. TYPE: Mauritius. Pétrin Nature Reserve: low *Philippia* heath formation, 630 m, 15 May 1979 (fl, fr), *Lorence 2631* (holotype, MO; isotype, K).

Glabrous dioecious shrub, rarely a small treelet, the multiple erect stems 50–200 cm tall and 6–10 mm diam., the mature leafy stems 2–4 mm diam., longitudinally striate. Leaves opposite, decussate, subsessile or sessile, glabrous; petiole 1–1.5 mm long by 2–3 mm wide; lamina subcoriaceous, ovate to elliptic, 30–80 by 25–55 mm, the apex shortly acute, obtuse or retuse, often rounded or mucronulate, the base cordate, rarely subtruncate, the secondary veins 5–6 pairs, making a 50–60° angle with the costa, the venation raised and visible to 3(–4°) adaxially and to 4(–5°) abaxially, the margin slightly revolute; seedling leaves heterophyllous, the petioles short, red when living, the lamina narrowly elliptic, entire or with 1–2 pairs of small teeth apically. Inflorescence glabrous, either ramiflorous on leafless nodes or cauliflorous, the flowers solitary or in fascicles of 2(–3), very rarely in a short di- or pleiochasium of 3(–5) flowers, or the flowers rarely solitary and axillary or terminal on leafy shoots. Androecious flower in bud globose, 10–16 mm diam., the apex with 4 minute, obtusely deltoid tepals, the pedicel and peduncle jointed basally, 9–30(–50) mm by 1–1.5 mm, bearing basally 1–3 pairs of apically ciliate, deltoid bracteoles; at anthesis 4(–5)-fid, 28–36 mm diam., the lobes spreading flat, then reflexing; stamens numerous, ca. 300–400, narrowly ellipsoid or clavate, 1–2 mm by 0.5–1 mm, the loculi occupying ½–¾ total length of the stamen, usually separate, sometimes confluent basally into a U-shape, or confluent apically at the obcordate apex, the connective not prolonged, the internal receptacle surface bearing scattered hairs. Gynoecious flower in bud napiform-depressed, apiculate with 4 minute tepals, the pedicel and peduncle jointed basally, 10–15 mm by 1–1.5 mm, basally bracteolate as in male flower; at anthesis shallowly napiform-urceolate, 8–12 mm diam. by 4–6 mm long, the orifice splitting into 4(–6) outcurved deltoid lobes, 5–8 mm diam., comprising ½–⅔ total width of the receptacle, the internal surface of the lobes shallowly rugose, glabrous; styles numerous, ca. 100–400, shortly conical, 0.8–1 mm long by 0.4–0.5 mm wide basally, the apex papillose, the internal receptacle surface with clusters of simple hairs between the styles. Fruiting receptacle solitary on the stems, patelliform to shallowly cupuliform, 25–60 mm diam. by 13–40 mm long, the orifice 16–40 mm diam., comprising ½–¾ total width of the receptacle, the rim subentire with 4–6 indurated deltoid lobes, the walls 8–12 mm thick, the external surface corky brown, the internal surface with numerous short, conical styles 0.5–1 mm long by 0.5 mm wide basally, interspersed with clusters of hairs, the pedicel and peduncle 16–25 mm by 2–3 mm. Mature carpels 12–13 mm long, 6–8 mm wide, 5–6 mm thick, ovoid-compressed, the endocarp dark brown, the surface scrobiculate. Gametic chromosome number, $n = 19$. Figure 42.

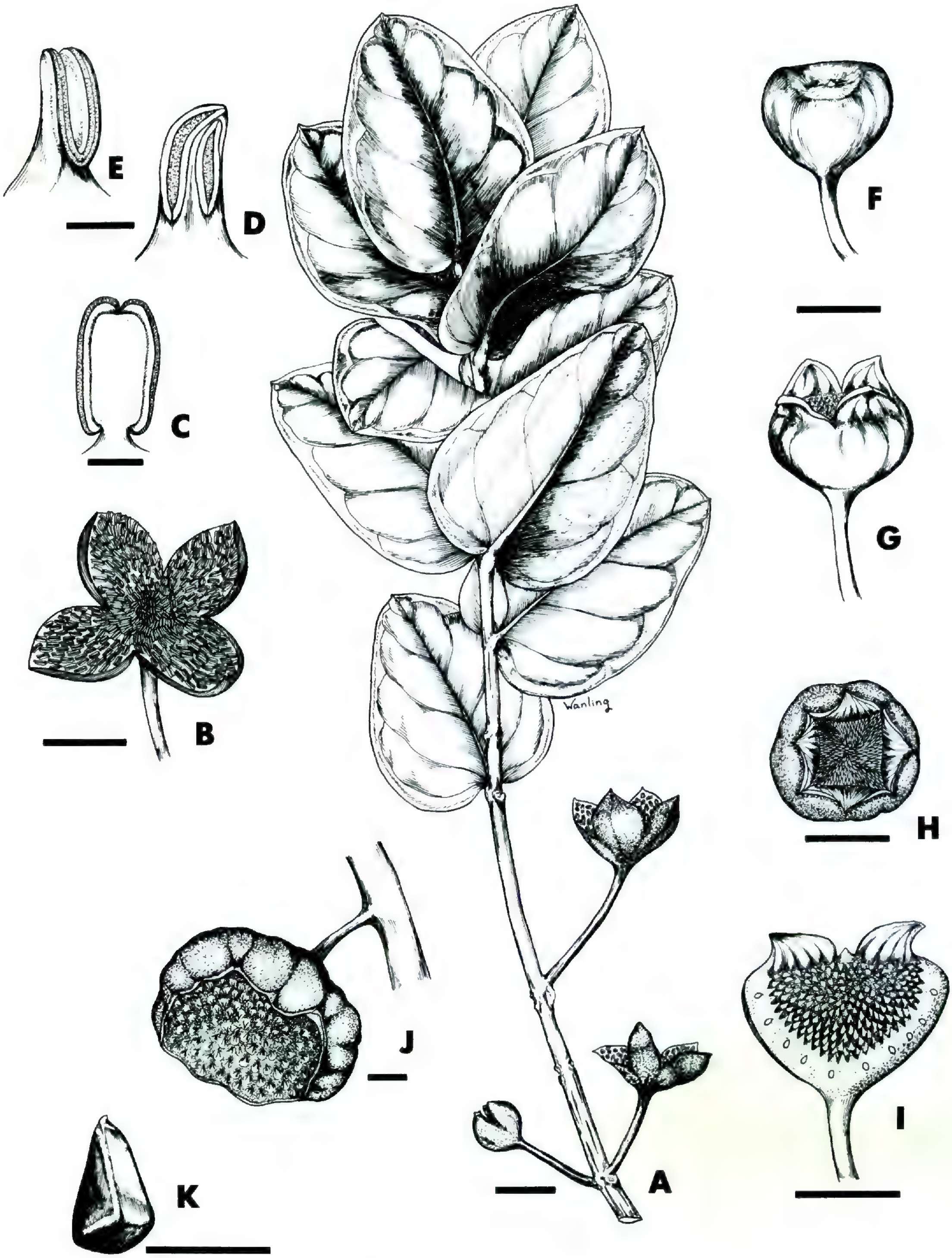


FIGURE 42. *Tambourissa cordifolia* Lorence.—A. Habit, male.—B. Androecious flower at anthesis, apical view.—C. Stamen with free loculi, abaxial view.—D. Stamen with free loculi, adaxial view.—E. Stamen with basally confluent loculi, adaxial view.—F. Gynoecious flower in bud, lateral view.—G. Gynoecious flower at anthesis, lateral view.—H. Gynoecious flower at anthesis, apical view.—I. Gynoecious flower at anthesis, longitudinal section.—J. Submature fruiting receptacle.—K. Fruiting carpel, lateral view. A–E. *Lorence 2632* (MO). F–I. *Lorence 2630* (MO). J, K. *Lorence 2631* (MO). Bars equal 10 mm in A, B, F–K, and 1 mm in C–E.

Distribution. Endemic to Mauritius (Fig. 40).

Habitat. *Tambourissa cordifolia* is restricted to upland regions of hard, unweathered ground water laterite or "cuirasse" supporting low scrub formations, often of *Philippia* heath. It is particularly abundant at Pétrin (630 m, annual precipitation 4,000 mm), and also occurs in comparable *Philippia* heath on Mt. Laselle (550 m, annual precipitation 4,500 mm), in low, marshy scrub at Les Mares near the base of Mt. Cocotte (650 m, annual precipitation 4,800 mm), at Crown Land Declerc, and in low thicket near the summit of Piton de la Rivière Noire (827 m, annual precipitation 4,200 mm).

MAURITIUS. CROWN LAND DECLERC: 15 Aug. 1968 (fl), *Vaughan sub MAU 13343* (MAU). LES MARES: track from Plaine Paule to Mt. Cocotte, 650 m, 13 May 1979 (fl), *Lorence 2626* (MO); 10 Aug. 1979 (fl), *Lorence 2894* (MO). MARE LONGUE PLATEAU: June 1977 (fl), *Friedmann 3132* (P). MONTAGNE LASELLE: N flank, 4 Oct. 1973 (fl), *Lorence sub MAU 16282* (MAU); Midlands, exposed situations, Mar. 1931 (fr), *Vaughan sub MAU 729* (MAU). PÉTRIN NATURE RESERVE: low indigenous thicket, 2 June 1971 (fr), *Guého sub MAU 14762* (MAU); *Phylica/Philippia* heath on lateritic soil, Oct. 1975 (fl), *Guého sub MAU 17585* (MAU, 2 sheets); indigenous thicket near Pétrin, 2,150 ft. (630 m), 23 Mar. 1963 (fr), *Lalouette sub MAU 10337* (MAU); low *Philippia* heath formation, 630 m, 23 Apr. 1973 (fl), *Lorence M 113* (K, MO); (fl, fr), *Lorence M 114* (K, 2 sheets; MO); 26 May 1973 (fl), *Lorence M 144* (K, MO); 12 Dec. 1978 (fr), *Lorence 2119* (MAU, MO); 10 Feb. 1979 (fr), *Lorence 2378* (MAU, MO, P); 4 Apr. 1979 (fl), *Lorence 2571* (MO); 15 Apr. 1979 (fr), *Lorence 2595* (MAU, MO); 9 May 1979 (fl), *Lorence 2618* (MO); 12 May 1979 (fl), *Lorence 2623* (MO); 15 May 1979 (fr), *Lorence 2630* (MO); (fl), *Lorence 2632* (MAU, MO); 22 May 1979 (fl), *Lorence 2645* (MO, P, Z); (fr), *Lorence 2646* (MO); 19 June 1979 (st), *Lorence 2660* (MO); 1 May 1976 (fl), *Richardson et al. 4074* (K); (fl), *Richardson et al. 4075* (K); (fr), *Richardson et al. 4076* (K); (fr), *Richardson et al. 4077* (K); Crown Land Pétrin, 17 June 1939 (fl), *Vaughan sub MAU s.n.* (MAU); (fr), *Vaughan 729* (MAU); Aug. 1937 (fl), *Vaughan sub MAU 1400* (MAU, 2 sheets); 6 June 1969 (fl, fr), *Vaughan sub MAU 13776* (MAU). PITON DE LA RIVIÈRE NOIRE: (fl), *Randabel sub MAU 679* (MAU). WITHOUT PRECISE LOCALITY: (st), right hand leafy collection only, *Anon. sub MAU 1314* (MAU).

Its sessile, cordate leaves and shrubby habit are presumably adaptations to the unique ecological niche which *Tambourissa cordifolia* occupies. Among other Mascarene species of the genus, it appears to be most closely allied to *T. amplifolia* in terms of floral morphology. Both are cauliflorous (rarely ramiflorous) species with long pedicellate, often solitary flowers, the androecious flowers being 4-fid, internally white, and having numerous clavate stamens, the gynoecious receptacles being napiform, opening by 4(–6) everted deltoid lobes, and having numerous short, conical styles interspersed with hairs. *Tambourissa amplifolia* is readily distinguishable by its larger habit, basal cauliflory, monoecy, pubescent inflorescences with longer pedicels and smaller floral receptacles, and very much larger, non-cordate petiolate leaves. Both belong to species Group 5.

The only other dioecious Mauritian species besides *Tambourissa cordifolia* is *T. peltata,* which has ternate to subalternate leaves and belongs to species Group 9. Although the two species are known to hybridize naturally, at least one such hybrid (*Lorence 2624,* MO) is highly sterile with ca. 95% aborted pollen grains.

In living material, the flower buds and outer surface of the receptacle are cream or yellowish flushed with purple-red. The inner, staminal surface of the androecious flowers and lobes of the gynoecious flowers are creamy white and the styles purple-red. Flowers of both sexes produce strong, fruity odors akin to that of ripe apricots or stewed ripe bananas.

Vernacular name. Bois tambour (Mauritius).

30. Tambourissa sieberi (Tul.) A.DC., Prodr. 16(2): 660. 1868; Baker, Fl. Mauritius 287. 1877; Perk. & Gilg, Pflanzenr. 4, 101: 68. 1901; Vaughan, Mauritius Inst. Bull. 1(1): 76. 1937. *Ambora sieberi* Tul., Ann. Sci. Nat. (Paris) 4(3): 31. 1855; Tul., Monogr. Monim. 304. 1855. TYPE: Mauritius. Without precise locality (ca. 1822) (fl), *Sieber Fl. Maurit. II, 316* (holotype, P; isotypes, G, K).

A. vestita Tul., Ann. Sci. Nat. (Paris) 4(3): 31. 1855; Tul., Monogr. Monim. 306. 1855. *Tambourissa vestita* (Tul.) A.DC., Prodr. 16(2): 660. 1868; Cordem., Fl. Réunion 301. 1895; Perk. & Gilg, Pflanzenr. 4, 101: 69. 1901. TYPE: "Bourbon?" (probably Mauritius), without precise locality (ca. 1755), *Commerson s.n.* (holotype, P).

Monoecious tree 10–15 m tall and 30–40 cm D.B.H., the bark light brown, flaking, the new growth velutinous-tomentose with simple, yellowish wavy hairs, the mature leafy stems velutinous, terete, 2–5 mm diam. Leaves opposite to subopposite, petiolate; petioles velutinous, 5–15 mm by 1–1.5 mm; lamina chartaceous to subcoriaceous, both surfaces tomentose-pubescent when young, adaxially glabrescent, elliptic to

broadly elliptic, rarely obovate or suborbiculate, 40–76 mm by 18–40 mm, the apex shortly acuminate, acute, rarely obtuse, the base acutely cuneate to acute, the secondary veins 4–7 pairs, making a 60–70° angle with the costa, the venation visible to 2(–3°) adaxially, and to 3(–4°) abaxially, the margin revolute. Inflorescence cauliflorous on mid to upper part of the trunk and on the major branches, an erect, generally unisexual, rarely leafy thyrse of 16–90 flowers, irregularly branching to 2(–3°), all parts pale yellowish velutinous-tomentose, the floral axis stout, 50–310 mm by 3–8 mm, flattened and dialated at the nodes, the secondary axes opposite to subopposite, ± ascendant, 6–90 mm by 2–4 mm, the ultimate branches bearing cymose units of 1–4 flowers, the buds of both sexes globose, 12–14 mm diam., velutinous, apiculate, the apex crowned with 2–3 pairs of persistent, decussate velutinous naviculate tepals 1.5–2.5 mm long by 1 mm wide, the pedicels and peduncles often subtended by a subulate, velutinous caducous bracteole 2–3 mm long, or rarely by a leaf, the pedicels 10–25 mm by 1.5–2 mm. Androecious flower at anthesis deeply (4–)5(–6)-fid, 25–35 mm diam., the lobes spreading flat; stamens numerous, ca. 100–140, ovoid to ellipsoid or oblong, 2–5 mm long by 1–2 mm wide, subsessile, the loculi lateral, separate, occupying almost the entire length of the stamen, the filament broad, short or sessile, the connective broad, slightly prolonged or not, the apex obtuse to emarginate, the internal receptacle surface glabrous. Gynoecious flower at anthesis globose, 15–18 mm diam., the orifice subcircular, 2–4 mm diam., with 4–6 irregular, shallow lobes; styles numerous, ca. 850–875, narrowly conical to setose, 3–4 mm long by 0.4–0.5 mm wide basally, coalescent into groups of 12–30, the internal receptacle surface densely velutinous between the styles. Fruiting receptacles produced on the trunk and major branches, in clusters of 3–15, the major axis 15–20 mm diam., woody, the secondary axis ca. 12 mm diam., the pedicel and peduncle 10–35 mm long by 6–15 mm diam., the receptacle irregularly globose-urceolate, depressed, 55–160 mm diam. by 35–75 mm long, the orifice small, comprising ca. ¼–⅓ total width of the receptacle, the walls 18–20 mm thick, externally pale corky brown, internally with numerous setose styles 2.5–3.5 mm long by 0.5–0.6 mm wide basally, the sides channelled, the surface sparsely tomentose between the styles. Mature carpels ovoid-compressed, 10–13 mm long, 6–7 mm wide, 4–5 mm thick, the smooth endocarp pale brown. Gametic chromosome number, $n = 19$.

Distribution. Endemic to Mauritius (Fig. 40).

Habitat. Isolated individuals and small populations of *Tambourissa sieberi* are known from mature wet forest at Macabé (660 m) and in the Black River Gorges (400–500 m) where the annual precipitation is ca. 3,200–3,400 mm, and also from low cloud forest on Mt. Cocotte (650–760 m, annual precipitation ca. 5,000 mm). Although the species appears to set fruit readily and several seedlings presumably of *T. sieberi* were found at Mt. Cocotte, no recent regeneration was observed at any of the other sites, undoubtedly due to severe competitional pressures exserted by vigorously invasive exotic species.

Although Tulasne thought that the sterile type of *Ambora vestita* may have been collected in Réunion (formerly Bourbon) by Commerson, he in fact questioned the origin of the specimen. Commerson actually did collect in Réunion (Ly-Tio-Fane, 1976), but a number of his other collections are wrongly labelled. I therefore suspect that the type of *Tambourissa vestita* is actually from Mauritius where he collected more extensively. That the type of *T. sieberi* lacks leaves also seems to have prompted Tulasne to describe the Commerson specimen as a new species. In any case, no tomentose *Tambourissa* has ever been subsequently collected or noted from Réunion (Cordemoy, 1895; Rivals, in herb.; Cadet, pers. comm.). Because the type of *T. vestita* is indistinguishable from material of *T. sieberi,* I consider the species synonymous and have chosen to retain the latter name because the type has flowers and is more widely distributed in herbaria.

MAURITIUS. BLACK RIVER GORGES: 1 Dec. 1933 (fl), *Carcenac sub MAU 794* (MAU); Crown Land Le Bouton in Black River Gorges, primary wet forest, ca. 400 m, 10 Jan. 1976 (fl), *Lorence 1585* (K, 2 sheets; MAU, 2 sheets; MO). MACABÉ FOREST: (fl) (prob. Dec. 1973), *Bernardi sub MAU 12873* (G, MAU); Plateau Macabé, 12 Mar. 1933 (fl), *Carcenac 48 sub MAU 1313* (MAU); Crown Land Macabé, 20 Jan. 1950 (fr), *Dulgeet sub MAU s.n.* (MAU); left hand side of path to Macabé plot, 20 Dec. 1965 (fr), *Forest Department sub MAU 11935* (*carpol. coll. 161*) (MAU); upland forest of Macabé (fr), *Forestry Dept. sub MAU s.n.* (MAU); in plot, 6 Jan. 1967 (fl), *Vaughan sub MAU 12498* (MAU); just outside of plot, 6 Jan. 1967 (fl), *Vaughan sub MAU 12499* (MAU, 2 sheets); in plot, 18 Jan. 1976 (fr), *Vaughan sub MAU 13092* (MAU, 2 sheets); 16 Feb. 1967 (fl), *Vaughan sub MAU 13094* (MAU); corner of plot near road, 11 July 1968 (fr), *Vaughan sub MAU 13229* (*carpol. coll. 187*) (MAU, 2 sheets); upland cli-

max forest of Macabé, 24 Nov. 1938 (st), *Wiehe sub MAU s.n.* (MAU). MONTAGNE COCOTTE: degraded forest, 2,200 ft. (760 m), 8 Nov. 1969 (fr), *Barclay 1693* (K); on crest, 9 Nov. 1969 (fr), *Guého sub MAU 14192* (*carpol. coll. 186*) (MAU); degraded forest on summit, 770 m, 1 Dec. 1978 (fl), *Lorence 1978* (MO); 4 Jan. 1979 (fl), *Lorence 2250* (K, MAU, MO, P); *Lorence 2251* (K, MAU, MO, P, REU, Z). WITHOUT PRECISE LOCALITY: 1865 (fl), *De Franqueville s.n. sub Herb. DeCandolle 16, 2: 660, no. 12* (G-DC; microfiche, MO); (fl), *Anon. sub Herb. Richard s.n.* (P); (fr), *Vaughan V 35 sub MAU spirit coll. 52* (MAU).

Tambourissa sieberi seems to be most closely related to *T. bathiei* from Madagascar, particularly in terms of floral morphology, which is discussed under the latter species. Both belong to species Group 6. Among Mauritian species, *T. sieberi* shares several features with *T. quadrifida,* including cauliflory, a thyrsic inflorescence structure, closed gynoecious floral receptacles which open by small apical pores, and similar strong, fermenting-fruity floral odors. *Tambourissa quadrifida* is totally glabrous, however, and appears to be more closely allied to the Madagascan *T. perrieri* (Group 7) than to *T. sieberi.*

A sterile collection of *Tambourissa* from northern Madagascar (*Baron 6720,* K) with similarly tomentose leaves, accompanied by a pencil sketch of a solitary, terminal fruit, apparently represents an undescribed species possibly allied to *T. sieberi.* Besides having solitary, terminal fruits, the leaves of *Baron 6720* differ from those of *T. sieberi* in containing numerous oil cells in the lamina and in having less densely branched ultimate veins. It is described as *Tambourissa* "sp. D" (no. 43) at the end of this treatment.

Flowers of *Tambourissa sieberi* are either bright yellow or dark purple, often within the same population. Floral odor in both sexes is strong and cloying, reminiscent of overripe or fermenting fruit.

Vernacular name. Bois tambour (Mauritius).

31. Tambourissa bathiei Cavaco, Bull. Soc. Bot. France 104: 284, fig. 1. 1957; Cavaco in Humbert, Fl. Madagascar 80: 20, fig. V:2–5. 1959. TYPE: Madagascar. Majunga: Firingalava, right hand tributary of the Ikopa River, W of Antsiafabositra (probably July 1899) (fl), *Perrier de la Bâthie 495-A* (holotype, P).

Monoecious tree, the new growth hirsute. Leaves (known only from the inflorescence) presumably opposite, petiolate; petioles 5–6 mm by 0.8 mm, hirsutulous; lamina chartaceous, elliptic, 40–58 mm by 20–25 mm, the apex shortly acuminate, the base acutely cuneate, the secondary veins 5–7 pairs, making a 65–70° angle with the costa, the venation prominent, visible to 4° on both surfaces, the margin plane. Inflorescence cauliflorous, unisexual, a condensed pleiochasium, or thyrse of (8–)20–34 flowers, sometimes leafy, the floral axis (20–)55–95 mm long by 3–4 mm wide medially, hirsutulous-pubescent. Androecious flower in bud globose, 10–13 mm diam., sparsely pubescent, apiculate with 3–4 minute, obtuse velutinous tepals, the pedicel 25–45 mm by 1.5–2 mm, subtended by a small, caducous ciliate deltoid bracteole 2 mm long; at anthesis deeply 3–4-fid, 25–35 mm diam., the lobes spreading ± flat; stamens numerous, ca. 350–450, clavate, 2–3 mm long by 1–1.5 mm wide, the filament well developed, comprising ca. ½–⅔ total length of stamen, the loculi apical, connivent or confluent at the obcordate-emarginate apex, occupying ca. ⅓–½ total length of stamen, the internal receptacle surface with clusters of short, dense hairs between the stamens. Submature gynoecious inflorescence a fulvous, velutinous-pubescent condensed pleiochasium of 8 flowers, the floral axis 24 mm by 2.5 mm. Submature gynoecious flower in bud globose, 7–8 mm diam., apiculate with 3–4 obtuse, velutinous tepals, the pedicel 12–15 mm by 1.5 mm; styles numerous, several hundred, completely lining the receptacle, narrowly conical, 1 mm long by 0.3–0.4 mm wide at the slightly ventricose base, the acuminate apex slightly papillose, the internal receptacle surface densely velutinous between the styles. Mature gynoecious flowers, fruiting receptacle, and carpels unknown.

Distribution. Endemic to Madagascar (Fig. 30).

Habitat. *Tambourissa bathiei* is known only from the type, which was collected along the Ikopa River, probably in riverine forest, in the Majunga province of western central Madagascar. The area formerly supported semideciduous dry forest of *Dalbergia* and *Commiphora,* but is now mainly savannah due to human disturbance.

On the basis of floral morphology, *Tambourissa bathiei* appears to be most closely related to *T. sieberi,* a species endemic to Mauritius, which also belongs to Group 6. Both species have small leaves, densely pubescent new growth, are cauliflorous with yellowish velutinous, generally

unisexual thyrses or pleiochasia, and globose gynoecious receptacles lined with numerous narrowly conical styles.

Although mature gynoecious flowers of *Tambourissa bathiei* are unknown, the buds are similar to those of *T. sieberi,* which open by a small, subentire apical pore only 1–2 mm diam. Androecious flowers of *T. bathiei* have numerous clavate stamens with long, distinct filaments and loculi connivent or confluent at the obcordate apex. In contrast, stamens of *T. sieberi* are broadly deltoid-ovate, sessile, and have separate lateral loculi along most of their length. Further collections, particularly mature gynoecious flowers and fruit, of this poorly known species are required. See discussion under species number 42.

32. Tambourissa perrieri Drake in Grandidier, Hist. Phys. Madagascar 1(1): 24. 1902; Perk., Pflanzenr. 4, 101 (Nachtr.): 42. 1911; Cavaco in Humbert, Fl. Madagascar 80: 30, fig. VIII:5–7. 1959. TYPE: Madagascar. Majunga: vicinity of Maevatanana, Ampassiri, 15 July 1899 (fl), *Perrier de la Bâthie 495* (holotype, P; isotypes, P, 2 sheets).

Monoecious shrub or tree 2–8 m tall, the bark smooth, dark, the branches spreading, the new growth sparsely pilose, glabrescent, the mature leafy stems pale green, smooth, glabrous, 2–2.5 mm diam. Leaves opposite, petiolate, glabrous; petioles 5–10(–20) mm by 1–2 mm; lamina chartaceous to subcoriaceous, both surfaces slightly lustrous, narrowly elliptic, narrowly ovate to narrowly oblong, 75–250(–280) mm by 27–50(–75) mm, the apex acuminate, the base acute to slightly obtuse, the secondary veins 7–13 pairs, making a 75–85° angle with the costa, the venation very prominent, finely reticulate, visible to 4(–5°) on both surfaces, the margin plane. Inflorescence cauliflorous on meristematic swellings on the trunk, ramiflorous or rarely terminal, a short, unisexual or sexually mixed pleiochasium of 7–9 flowers, the floral axis glabrous or with scattered hairs, 55–125 mm by 2–4 mm, each pedicel subtended by a broadly deltoid, ciliate bracteole. Androecious flower in bud globose, 9–11 mm diam., smooth, glabrous or with rare, scattered hairs, apiculate with 4 small, thick hirsutulous deltoid tepals, the pedicel 10–32 mm by 1–1.5 mm, with scattered hairs; at anthesis deeply 4-fid, 18–25 mm diam., the lobes spreading flat; stamens numerous, ca. 150–200, ovoid to obovoid or clavate, 1.8–3 mm long by 1.2–1.5 mm wide, more or less recurved, subsessile or the filament comprising up to ½ total length of the stamen, the loculi confluent at the obtuse apex or separate, the connective retuse, not prolonged, the internal receptacle surface with scattered to clustered short, simple hairs between the stamens. Gynoecious flower in bud obovoid to obpyriform, 9–11 mm long by 6–7 mm wide, ± glabrous or with a few hairs basally, apiculate with 4–5 small, thick hirsutulous deltoid tepals, the pedicel stout, tapered, 3–15 mm by 1.5–2 mm wide medially; at anthesis obovoid to obpyriform, 12–14 mm long by 7–9 mm wide, the apex shallowly 4–5-fid, the lobes thick, erect, deltoid, the orifice 3–6 mm diam., comprising ca. ½ total width of the receptacle; styles numerous, ca. 200, crowded, shortly conical, 5-angled, 0.5–0.7 mm long by 0.5 mm diam. at the slightly ventricose base, the apex shortly acuminate, the internal receptacle surface densely velutinous with short, white hairs between the styles and on inner surface of the lobes. Fruiting receptacle solitary, borne on the trunk or branches, rarely terminal, obovoid, subglobose or rarely cupuliform, 50–150 mm long by 35–130 mm wide, externally grayish, corky, smooth or venose, the orifice comprising $\frac{1}{10}$–$\frac{1}{5}$ total width of fruit, the styles conical; pedicel and peduncle 28–45 mm by 6–10 mm. Mature carpels ovoid-compressed, 8–10 mm long by 7–8 mm wide, the endocarp brown.

Distribution. Endemic to Madagascar (Fig. 30).

Habitat. *Tambourissa perrieri* appears to be commonest in the northwestern sector of Madagascar (the Diego Suarez, Sambirano and Majunga regions) where it apparently occurs in vegetation types ranging from semideciduous sclerophyllous moist forest of *Uapaca*/Chlaenaceae and dry forest of *Dalbergia/Commiphora/Hildegardia,* frequently along rivers, to wet forest of *Tambourissa/Weinmannia.* As most collections lack precise data, it is often difficult or impossible to determine the exact habitat. In addition, two collections of what appear to be *T. perrieri* (but differ in having cupuliform fruits) are known from the lower limits of the *Tambourissa/Weinmannia* zone (ca. 900 m) of the eastern domain at Analamazaotra near Perinet, a seemingly disjunct distribution pattern possibly attributable to undercollecting.

MADAGASCAR. DIEGO SUAREZ: Manongarvio Massif W of Sambirano River, above 510 m, Apr. 1909 (fr), *Perrier de la Bâthie 10116* (P); Sambirano, Feb. 1923

(fr), *Perrier de la Bâthie 15465* (P). MAJUNGA: Bemarivo River Bassin, Boina, 300 m, Aug. 1907 (fl), *Perrier de la Bâthie 10125* (P); Mt. Bekolosy, near Maormandla, Mar. 1909 (fr), *Perrier de la Bâthie 10117* (P). TAMATAVE: near Analamazaotra, 800 m, 1912 (st), *Perrier de la Bâthie 10128* (P); Maromisaba, near Analamazaotra, 1,000 m, Feb. 1921 (fr), *Perrier de la Bâthie 15958* (P).

Morphologically, *Tambourissa perrieri* most closely approaches *T. quadrifida* from Mauritius, the only other member of Group 7. Both species are cauliflorous, rarely ramiflorous or terminal, with unisexual or sexually mixed pleiochasia or thyrses produced along most of the length of the trunk. Androecious flowers of both split deeply into four flat or recurved segments bearing numerous short stamens. The gynoecious flowers of both are obovoid to obpyriform or ellipsoid with a small orifice; it is much smaller (1–2 mm diam.) in *T. quadrifida* which also has thicker, obtuse or retuse leaves with more obscure venation. Both species occur in relatively dry habitats and form a group apparently not closely allied to other members of the genus, with the possible exception of Group 6.

Vernacular name. Ambora-lavaravina (Madagascar).

33. Tambourissa quadrifida Sonn., Voy. Ind. Oriental ed. 1, 2: 237, tab. 134. 1782; ed. 2, 4: 405, tab. 134. 1806; Gmel., Syst. Nat. 2(1): 16. 1791; A.DC., Prodr. 16(2): 658. 1868; Baker, Fl. Mauritius 288. 1877; Perk. & Gilg, Pflanzenr. 4, 101: 71. 1901, excl. synon. *T. obovata*; Drake in Grandidier, Hist. Phys. Madagascar 1(1): 21. 1902, pro parte, excl. synon. *T. purpurea, T. rota, T. parvifolia*; Perk., Pflanzenr. 4, 101 (Nachtr.): 41. 1911. *Mithridatea quadrifida* (Sonn.) Comm. ex Schreb., Gen. Pl. 2: 783. 1791; Willd., Sp. Pl. 1(1): 27. 1797; Spreng., Syst. 5(3): 866. 1826. *Ambora quadrifida* (Sonn.) Poir., Encycl. 7: 565. 1806; Tabl. Encycl. 784. 1806; Tul., Monogr. Monim. 297. 1855. TYPE: Ile de France (Mauritius). Without precise locality (ca. 1775) (fl), *Commerson s.n. sub Herb. A. L. de Jussieu 16708* [lectotype, P-JUSS, here designated (photo, MO); isolectotypes, P-JUSS (photos, MO), both mixed with *T. elliptica* subsp. *micrantha*].

Ambora sempervirens F. G. Dietr., Lexic. Gart. 1: 342. 1802, nom. superfl., based on *T. quadrifida*.

A. tambourissa Lam. ex Steud., Nom. Bot. 37. 1821, nom. superfl., non *A. tamburissa* Boiv. ex Tul.

Mithradatea tamburissa Bojer, Hortus Maurit. 290. 1837, nom. superfl., based on *T. quadrifida*.

Ambora neglecta Tul., Monogr. Monim. 432. 1855. *Tambourissa neglecta* (Tul.) A.DC., Prodr. 16(2): 659. 1868; Perk. & Gilg, Pflanzenr. 4, 101: 71. 1901. TYPE: Mauritius. July 1855, *Labillardiere s.n.* (lectotype, P, here designated).

Monoecious to subdioecious tree attaining 15 m tall, the stems often multiple, to 15–30 cm D.B.H., the bark light brownish gray, flaking or checking, the new growth totally glabrous, the mature leafy stems glaucous, smooth to longitudinally striate, 2–4 mm diam. (suckers to 7–8 mm diam.). Leaves opposite to subopposite (sometimes alternate on suckers), petiolate, glabrous; petioles 5–12 mm by 1–1.5 mm; lamina subcoriaceous, broadly to narrowly elliptic, oblong or obovate, (30–)45–100 mm by (13–)17–52 mm, the apex shortly acute to mucronate, obtuse, rounded or retuse, the base acutely decurrent to acutely cuneate, the secondary veins 4–8 pairs, making a 55–65° angle with the costa, the venation ± obscure adaxially, visible to 2–3° on both surfaces, the margin plane to slightly revolute. Inflorescence a glabrous, generally ± unisexual, sometimes leafy, condensed pleiochasium or sparsely branching thyrse of (3–)5–35(–110) flowers, cauliflorous on meristematic swellings along the entire length of the trunk, or the flowers rarely solitary on leafless nodes or axillary, the floral axis (30–)40–180 mm by 2–4 mm, the flowers borne singly or in cymose units of 2–3. Androecious flower in bud smooth, obovoid to ellipsoid, 10–20 mm long by 7–10 mm wide, apiculate with 3–4 minute, glabrous, obtuse-deltoid tepals, the pedicel 10–30 mm by 1–1.6 mm, occasionally jointed to a distinct peduncle up to 12 mm long, often subtended by an obtuse, ciliate bracteole 0.5 mm long by 0.5–1 mm wide; at anthesis deeply (3–)4-fid, splitting deeply to the base, 20–32 mm diam., the lobes ultimately completely reflexed; stamens numerous, ca. 300–500, ellipsoid to oblong, 1.5–2.5 mm long by 0.8–1.4 mm wide, the filament distinct, comprising ca. ¼–⅓ total length of the stamen, the connective emarginate to slightly apiculate, the internal receptacle surface with scattered clusters of short hairs between the stamens. Gynoecious flower in bud obovoid to ellipsoid, 10–16 mm long by 7–10 mm wide, smooth, glabrous, apiculate with 3–4 minute deltoid tepals,

the pedicel 7–10 mm by 1.5–2 mm, sometimes jointed to a peduncle attaining 10 mm long, often subtended by a minute bracteole; at anthesis with a subentire, shallowly 3–5-fid orifice 1–2 mm diam., the thick deltoid lobes straight or scarcely outcurved; styles numerous, ca. 200–300, lining the receptacle except near the apex, shortly conical, 0.4–0.6 mm long by 0.6 mm diam. at the abruptly swollen base, the internal receptacle surface velutinous between the styles and on the lobes, the dense hairs short, the external surface soon becoming corky. Fruiting receptacles borne on the trunk and major branches, solitary or in clusters of 2–3, irregularly obovoid-pyriform to globose-urceolate and depressed, 50–170 mm long by 50–100 mm diam., the walls 16–25 mm thick, externally corky brown, the orifice small, 5–10 mm diam., comprising ca. $\frac{1}{10}$ total width of fruit, the internal surface with numerous, scattered shortly conical styles 0.7–0.8 mm long by 0.3–0.4 mm wide basally, the pedicel and peduncle stout, 10–20 mm long by 7–18 mm diam. medially. Mature carpels ovoid-compressed, 13–19 mm long, 7–13 mm wide, 5–7 mm thick, the endocarp pale to dark brown, the surface minutely scrobiculate-rugose. Gametic chromosome number, $n = 19$.

Distribution. Endemic to Mauritius (Fig. 38).

Habitat. *Tambourissa quadrifida* is restricted to the western escarpments of the central plateau, ranging from the Trois Mamelles mountain range in the north to the mountains opposite Le Morne Brabant in the south. It is local and occasional to common in evergreen or semideciduous moist forest of *Elaeodendron orientale* Jacq., *Diospyros* spp., *Mimusops petiolaris* Dubard, and other species characteristic of the relatively dry rain shadow area. Although older trees of *T. quadrifida* are still relatively common, I observed no recent regeneration of the species, possibly due to grazing pressures from the high populations of stag which are maintained in the region for hunting.

MAURITIUS. CHAMAREL: Chamarel Hill, near first hairpin bend by roadside on edge of mountain reserves, 600 ft. (ca. 200 m), 19 Apr. 1939 (fl), *Vaughan V 1512* (MAU, 5 sheets); Chamarel, Dec. 1937 (st), *Vaughan 1512A* (MAU). PITON DU FOUGE: W flank, dry forest, ca. 400 m, 9 Aug. 1975 (fl), *Lorence 1337* (K, 2 sheets; MAU); flank of mountain ridge facing Le Morne Mt. and overlooking Coteau Raffin Village, 9 Aug. 1975 (fl), *Guého sub MAU 17356* (MAU). TROIS MAMELLES MT.: dense forest near Trois Mamelles, Aug. 1928 (fl), *Vaughan 544* (K). YEMEN MATALA VALLEY: under Brise Fer Mountain, dry forest (st), *Bernardi 14846* (G); 4 Dec. 1973 (fl), *Coode et al. 4270* (K, 2 sheets; MAU); W foothills of Brise Fer Mt., Yemen, Matala Valley, 17 Jan. 1976 (fr), *Lalouette sub MAU 17744* (MAU); 17 Mar. 1979 (fl, fr), *Lorence & Lalouette 2538* (K, MO, P, REU, Z); (fl), *Lorence & Lalouette 2539* (MO); 31 May 1979 (fl), *Lorence 2654* (K, MO, P, Z); (fl), *Lorence 2655* (K, MO, P); (fl), *Lorence 2656* (MO, REU); Yemen estate, 4 July 1968 (fl), *Maingard sub MAU 13266* (MAU); by side of road at Yemen, 4 July 1968 (fl, fr), *Vaughan sub MAU 13215* (*carpol. coll. 178*) (MAU, 4 sheets). WITHOUT PRECISE LOCALITY: (st), *Anon. 4663* (G, K); (fl), *Anon. sub Herb. Delessert s.n.* (G); (fl), *Anon. sub Herb. DeCandolle 16(2): 658* (G-DC, 2 sheets; microfiche, MO); (st), *Anon. sub Herb. Richard s.n.* (P, left hand collections only); *Anon. sub Herb. Richard 111* (P, 2 sheets); (fl), *Ayres s.n.* (K); (fl), *Bojer s.n.* (K); 1831 (fl), *Bouton s.n.* (P); 1814 (fl), *Carmichael s.n.* (K); (fl), *Ilardwicke 6* (G); (st), *Martin s.n.* (G); (fl), *Martin 607* (G, 2 sheets).

Tambourissa quadrifida appears to be most closely allied to *T. perrieri* from Madagascar, also of species Group 7. The latter is distinguishable by its globose androecious flower buds, gynoecious flowers with larger orifices (3–4 mm diam.), longer, acuminate leaves with more prominent venation, and floral ground tissue with abundant oil cells lacking in *T. quadrifida*.

Living flowers produce a strong odor of ripe fruit similar to that of *Tambourissa sieberi*. Two floral color morphs occur in the population at Yemen, the androecious flowers being either tomato red or salmon orange, whereas the gynoecious flowers have either red or greenish white to pink styles. Buds and outer receptacle surfaces are marbled green, often flushed with red.

Vernacular names. Bois tambour, Pomme de singe (Mauritius).

34. Tambourissa alaticarpa Lorence, nom. nov. *Phanerogonocarpus perrieri* Cavaco, Bull. Soc. Bot. France 104: 613. 1957; Cavaco in Humbert, Fl. Madagascar 80: 4. 1959 non *Tambourissa perrieri* Drake in Grandidier, Hist. Phys. Madagascar 1(1): 24. 1902. TYPE: Madagascar. Tamatave: E coast, bank of the Fandrarazana River, 200 m, 1930 (fl), *Perrier de la Bâthie 10102* (holotype, P).

Monoecious treelet, the new growth pale yellowish villous, the hairs simple, the submature stems 3 mm diam., stramineate, villous. Leaves opposite, petiolate; petioles 15–16 mm by 2 mm, villous; lamina chartaceous, elliptic to oblong, 210–220 mm by 75–80 mm, the apex abruptly acuminate, the base cuneate, adaxially sparsely

pilose, abaxially densely pilose, the costa velutinous, depressed adaxially, prominent abaxially, the secondary veins ca. 7 pairs, making a 50–60° angle with the costa, festooned brochidodromous, the venation raised and visible to 3–4° on both surfaces, the margin serrate-dentate with 9–10 pairs of narrowly acute, antrorse teeth ca. 1 mm long, the tips glandular, indurated. Apparently cauliflorous (also ramiflorous?), the inflorescence either a sexually mixed pleiochasium 150–250 mm long with 7–10 lateral androecious flowers and a single, terminal gynoecious flower, the floral axis 100–240 mm by 1.5–3 mm, pilose to velutinous, or a short, unisexual pleiochasium 20–30 mm long of 7–10 androecious flowers, the floral axis 6–20 mm by 0.5–1 mm, pilose to villous. Androecious flower in bud glabrous or with rare, scattered hairs, obovoid to ellipsoid, 4–5 mm by 3–3.5 mm, apiculate, the apex with 3–4 acute, scarious deltoid tepals 0.5 mm long and wide, the pedicel 13–19 mm by 0.5 mm, sparsely pilose, subtended by a subulate-linear bracteole 2–3 mm long; at anthesis deeply 4-fid, 7–9 mm diam., the lobes spreading flat; stamens ca. 38, clavate, 1.2–1.6 mm long by 0.7–0.8 mm wide, the filament distinct, stout, the loculi separate, lateral or oblique, occupying ¼–½ total length of the stamen, the connective obtuse or apiculate, scarcely or not prolonged, the internal receptacle surface glabrous. Gynoecious flower terminal, sparsely pilose or glabrate, in bud narrowly obovoid, tubular, 22–28 mm by 4–5 mm, angular with 4–6 longitudinal wings 1–1.5 mm wide running from apex to pedicel, the apex crowned by 6–8 subulate tepals 1–1.5 mm long, the wall ca. 0.5 mm thick, the pedicel scarcely differentiated, 20–25 mm by 1.5 mm diam. medially; at anthesis apparently opening by a small (ca. 1 mm diam.) apical orifice flanked by several deltoid lobes; styles numerous, ca. 250–300, sharply conical, 1 mm long by 0.5 mm diam. basally, acuminate, curved antrorsely, the internal apical portion of the receptacle velutinous with short, simple white hairs, the styles interspersed with short, dense hairs. Fruiting receptacle probably resembling that of *T. longicarpa* (i.e., cylindrical, narrowly winged), the fruiting carpels (fide Perrier de la Bâthie) embedded in the orange receptacular tissue, the mesocarp red, the endocarp black.

Distribution. Endemic to Madagascar (Fig. 24).

Habitat. Presumably from lowland wet forest of Myristicaceae/*Anthostema,* the species is known only from the type.

Along with *Tambourissa longicarpa, T. alaticarpa* comprises the very natural species Group 8, characterized by elongate, narrowly winged gynoecious flowers and fruits. It differs from the former species in having larger, more sparsely pubescent leaves with smaller, more numerous teeth (only 2–3 pairs in *T. longicarpa*), and externally sparsely pilose to glabrate buds and flowers.

35. **Tambourissa longicarpa** Lorence, nom. nov. *Phanerogonocarpus capuronii* Cavaco, Bull. Soc. Bot. France 104: 612, figs. 1–4. 1957; Cavaco in Humbert, Fl. Madagascar 80: 3, fig. I:1–6. 1959 non *Tambourissa capuronii* Cavaco, Bull. Mus. Hist. Nat. (Paris), Ser. 2, 29: 287. 1957. TYPE: Madagascar. Diego Suarez: Atondradama Pass, N of the Masoala Peninsula, E forest, ca. 500 m, 22 Dec. 1953 (fl, fr), *Capuron 8775-SF* (holotype, P).

Large monoecious treelet, the new growth pale yellowish villous, the hairs simple, the mature leafy stems fulvous velutinous, 2–3 mm diam. Leaves opposite, petiolate; petiole 10–13 mm by 1.5–2 mm, fulvous velutinous; lamina broadly elliptic, 75–105 mm by 43–65 mm, chartaceous, the apex deltoid, acute, the tip thickened, the base cuneate, the adaxial surface sparsely pilose, especially along the costa and veins, glabrescent, the abaxial surface densely pilose with pale yellowish white hairs, especially along the costa and veins, the costa depressed adaxially, prominent and rounded abaxially, the secondary veins 5–6 pairs, making a 45–55° angle with the costa, the basal pairs festooned brochidodromous, the apical ones often excurrent into the marginal teeth, the venation visible to 2° adaxially and to 3° abaxially, the margin slightly revolute, strongly dentate in the apical ⅓ with (1–)2–3 pairs of broadly deltoid teeth 3–5 mm long, the tips thickened, glandular. Inflorescence basally cauliflorous, produced on meristematic swellings from the trunk, either a sexually mixed, 15–22 flowered pleiochasium with 1–3 terminal gynoecious flowers, the androecious flowers lateral in opposite to subopposite pairs or cymose groups of 2–3, the floral axis velutinous, 70–95 mm by 1–1.8 mm, subtended by several deltoid bracteoles, or a smaller unisexual pleiochasium of 7–

9 androecious flowers, the floral axis 18–35 mm by 1 mm. Androecious flower in bud hirsute, globose, 4–5 mm diam., apiculate with 1(–2) pairs of minute, subulate-deltoid tepals 0.3–0.5 mm long, the pedicel 10–22 mm by 0.5 mm, pilose, subtended by a subulate-naviculate, pilose bracteole 1 mm long; at anthesis deeply 4-fid, 9–11 mm diam., the lobes spreading flat, ultimately reflexing, each bearing 2–3 minute, fleshy tepals apically within; stamens 40–50, subulate, 1.5–2.5 mm long by 0.8–1 mm wide, the filament distinct, thick, the loculi separate, lateral or abaxially ± unifacial, 1–1.5 mm long, occupying ca. ½ total length of stamen, the connective prolonged, acute to apiculate, the inner receptacle surface with scattered hairs between the stamens. Gynoecious flower in bud narrowly obconical, tubular, 30–35 mm by 3.5–4 mm, ± quadrangular with 4(–5) lateral longitudinal wings ca. 1 mm wide, fulvous hirsute-velutinous, the apex bearing 4–6 deltoid-subulate hirsute tepals 1–2 mm long, the receptacle wall ca. 1 mm thick, the pedicel tapered, scarcely differentiated from the receptacle, 20–25 mm by 1 mm, hirsute, subtended by 2 subulate bracteoles 2–3 mm long; at anthesis opening by 4 deltoid lobes, the orifice ca. 1 mm diam.; styles numerous, ca. 500, crowded, conical, 0.4–0.5 mm long by 0.3 mm wide basally, the base slightly ventricose, the internal receptacle surface apically velutinous, the cavity ca. 2–2.5 mm diam., the styles interspersed with numerous short hairs, a mucilaginous exudate present. Fruiting receptacle pendulous, cylindrical-ellipsoid, 160 mm by 70 mm, externally pale corky brown, bearing 4–5 longitudinal wings, 4–5 mm wide, the orifice narrow, at maturity splitting lengthwise and exposing the central tube bearing part of the carpels, the pedicel and peduncle ca. 120 mm by 6 mm. Mature carpels ovoid-compressed, 12 mm by 5–6 mm, the mesocarp thin, red-orange, fleshy, the endocarp brown, minutely foveolate.

Distribution. Endemic to Madagascar (Fig. 24).

Habitat. The type and only known collection is from the eastern lowland Myristicaceae/*Anthostema* wet forest zone.

Most closely allied to *Tambourissa alaticarpa,* the only other member of species Group 8, *T. longicarpa* differs by its smaller leaves with fewer, much larger teeth, its more densely villous inflorescence and flowers, and by its stamens with the connective prolonged beyond the anther. Further collections and field studies are greatly desired.

36. Tambourissa castri-delphinii Cavaco, Bull. Soc. Bot. France 104: 283. 1957; Cavaco in Humbert, Fl. Madagascar 80: 32, fig. IX:9–10 (non fig. VIII). 1959. TYPE: Madagascar. Tulear: Ebakika, Fort Dauphin district, in secondary forest (savoka), small tree, 17 Nov. 1932 (fl), *Decary 11052* (holotype, P).

Small monoecious or subdioecious trees 5–7 m tall, the mature leafy stems terete to subtrigonous, 3–7 mm diam., glabrous, stramineate. Leaves ternate, rarely opposite, petiolate, glabrous; petioles 7–13 mm by 1.5–2 mm; lamina subcoriaceous, both surfaces moderately lustrous, ovate to oblong, 88–170 mm by 38–68 mm, the apex abruptly and shortly acuminate, the base acutely cuneate, the secondary veins 5–7 pairs, making a 45–50° angle with the costa, the venation raised and prominent, visible to 4° on both surfaces, the margin thickened, slightly revolute. Androecious inflorescence ramiflorous, axillary on the leafless nodes, a contracted pleiochasium or fascicle of 4–9 flowers, the floral axis 1–9 mm by 1.5–2 mm, sparsely puberulent basally, subtended by several pale, naviculate-deltoid, ciliate bracteoles 0.5–1.5 mm long. Androecious flower in bud glabrous, globose, 9–18 mm diam., apiculate with 4–6 short, obtuse tepals, the pedicel 10–18 mm by 0.8–1 mm, subtended by a bracteole; at anthesis deeply 4–5-fid, 25–32 mm diam., the lobes spreading flat, reflexing, purple within; stamens numerous, ca. 200–300, ovoid to deltoid, thin, 2.5–4 mm long by 1.5–2 mm wide, the filament short, subsessile, the loculi lateral, confluent at the obtuse apex, rarely free, the connective not prolonged, the internal receptacle surface with scattered or clustered simple hairs between the stamens. Gynoecious flowers presumably ramiflorous like the male, at anthesis napiform-depressed, 4–6 mm long by 10–14 mm diam., externally glabrous, internally densely hirtellous on the lobes, the orifice small, X-shaped, the styles numerous, ca. 800–900, conical acuminate, 0.7–0.9 mm long and wide basally, interspersed with numerous hairs; pedicel and peduncle 8 or more mm long. Mature fruiting receptacle subglobose-cupuliform, 40–45 mm long by 40–60 mm wide, externally corky, the walls 10–12 mm thick, the orifice comprising ca. ¼–½ total width of fruit,

the styles conical 0.8–1.5 mm by 0.8 mm, interspersed with rare hairs; pedicel and peduncle 17 mm by 5 mm. Mature carpels ovoid-compressed, 10–11 mm by 5–8 mm, pale tan.

Distribution. Endemic to Madagascar (Fig. 30).

Habitat. *Tambourissa castri-delphinii* is known only from the SE coastal region between Mananjary and Fort Dauphin. Capuron notes that the species occurs in coastal "savoka" (secondary or disturbed primary forest) over old sand dunes.

MADAGASCAR. FIANARANTSOA: Mananjary, Mar.–Apr. 1909 (fr), *Geay 8287* (P). TULEAR: between Fort Dauphin and Manantenina, near Manambato (fl), *Capuron 28667-SF* (P); Ebakika, 18 Nov. 1932 (fl), *Decary s.n.* (P); Mendena, 16 Feb. 1949 (fr), *Capuron 378-SF* (P); Fort Dauphin, Manambato, 12 Dec. 1972 (fl), *Jacquenim 1197* (P).

Cavaco (1957b) states that *Tambourissa castri-delphinii* is related to *T. religiosa,* also Madagascar, because leaves of both species are similarly subcoriaceous or coriaceous with prominent venation. This similarity is most likely because both species occupy a similar habitat in coastal forest. More significantly, adult phyllotaxis is different, being opposite in *T. religiosa* and usually ternate in *T. castri-delphinii,* the latter character otherwise found only in *T. ficus* and *T. peltata,* both Mauritian endemics. In addition, venation of all three ternate-leaved species is prominent and finely reticulate, showing a high degree of organization. Furthermore, androecious flowers of *T. religiosa* and *T. castri-delphinii* are totally different. Both *T. peltata* and *T. castri-delphinii* are cauliflorous or ramiflorous on the upper branches, producing large, deeply 4(–5)-fid androecious flowers with recurved segments and numerous, broadly ovoid to deltoid subsessile stamens, whereas those of *T. religiosa* are small and globular with fewer, much smaller stamens. For these reasons *T. peltata* and *T. castri-delphinii* appear to be more closely related and I have placed them together in species Group 9.

Tambourissa peltata differs from *T. castri-delphinii* by its larger, solitary or paired androecious flowers with thicker pedicels, and discoid female receptacle with broad, sterile lobes and columnar styles. Gynoecious flowers of *T. castri-delphinii* differ from both *T. ficus* and *T. peltata* in having an X-shaped orifice.

37. Tambourissa ficus (Tul.) A.DC., Prodr. 16(2): 659. 1868; Perk. & Gilg, Pflanzenr. 4, 101: 69, fig. 18Q. 1901; Perk., Gatt. Monim. fig. 34Q. 1925. *Ambora ficus* Tul., Ann. Sci. Nat. (Paris) 4(3): 30. 1855; Tul., Monogr. Monim. 300. 1855. TYPE: "Java" (probably Mauritius). Without precise locality (ca. 1800) (fl), *Leschenault de la Tour s.n.* (holotype, P).

Ambora alternifolia Tul., Ann. Sci. Nat. (Paris) 4(3): 31. 1855; Tul., Monogr. Monim. 305. 1855. *Tambourissa alternifolia* (Tul.) A.DC., Prodr. 16(2): 660. 1868; Baill., Adansonia, Ser. 1, 9: 131. 1868–1870; Perk. & Gilg, Pflanzenr. 4, 101: 72. 1901; Cavaco, Bull. Soc. Bot. France 104: 284. 1957. TYPE: Ile Maurice (Mauritius). At the foot of the Pouce, above the plain at Moka, Oct. 1849, *Boivin s.n.* [lectotype, P, here designated, as to androecious floral buds only, excluding the stem and leaves which are *Homalium integrifolium* (Lam.) Baill. (Flacourtiaceae)].

Ambora obovata Tul., Ann. Sci. Nat. (Paris) 4(3): 31. 1855; Tul., Monogr. Monim. 306. 1855. *Tambourissa obovata* (Tul.) A.DC., Prodr. 16(2): 660. 1868; Perk. & Gilg, Pflanzenr. 4, 101: 70. 1901. TYPE: Ile Maurice (Mauritius). Woods of the Pouce, Sept. 1849, *Boivin s.n.* (holotype, P).

T. elliptica sensu Baker, Fl. Mauritius 288. 1877; sensu Perk., Pflanzenr. 4, 101 (Nachtr.): 44. 1911 non (Tul.) A.DC.

Ficus sapotoides Baker, Fl. Mauritius 284. 1877. TYPE: Mauritius. Pouce above plateau, Sept. 1862, *Ayers s.n.* (holotype, K; photo, P).

Monoecious to subdioecious treelet or tree 10–15 m tall and 10–15 cm D.B.H., the base of the trunk frequently swollen, the new growth finely pilose to fulvous tomentose, the mature leafy stems glabrous, stramineate, subterete, 2–5 mm diam. Leaves ternate to subalternate, rarely opposite to subopposite, petiolate, glabrous; petioles 10–25 mm by 1.5–2 mm (to 45 mm long on vigorous suckers); lamina chartaceous to subcoriaceous, broadly to narrowly obovate, oblanceolate, narrowly to broadly elliptic, 60–150 (–180) mm by (20–)30–75 mm (to 170 mm by 100 mm on vigorous suckers), the apex acuminate, acute, obtuse or retuse, the base acutely decurrent to acutely cuneate, the secondary veins 5–8(–11) pairs, making a 50–70° angle with the costa, the venation finely reticulate, prominent, visible to 3–4° adaxially and to 4° abaxially, the margin plane to slightly revolute; juvenile and sucker leaves often heterophyllous, the petioles red when living, the lamina apically serrate-dentate with 1–3 pairs of teeth. Inflorescence cauliflorous on the swollen base of the trunk, sometimes extending up the lower portion of the trunk for several meters or rarely on the leafless parts

of the lower branches, the flowers solitary or in fascicles of 2(–3) on the meristematic swellings. Androecious flower in bud globose-depressed to napiform-depressed, 20–30 mm diam. by 15–25 mm long, pubescent, smooth to corky, longitudinally ribbed basally, the walls thick and fleshy, apiculate with 3–5 minute, hirsute tepals, the pedicel stout, tapered, jointed near the base, the pedicel and peduncle 15–25 mm by 3–4.5 mm diam. medially, pubescent to velutinous, bearing several hirsute, subulate-naviculate bracteoles 1–2 mm long; at anthesis shallowly to deeply 4–6(–7)-fid, either partially closed and urceolate, 20–40 mm diam. by 17–30 mm long, or the lobes spreading flat open, 35–75 mm diam.; stamens very numerous, ca. 900–1,800, curvate, linear to ellipsoid or ligulate, 3–6 mm long by 0.5–1 mm wide, the filament basally thickened, comprising ¼–⅓ total length of the stamen, the loculi separate, parallel, lateral, or abaxially ± unilateral and extrorse, comprising ca. ⅓ total length of the stamen, the connective thick, apically prolonged, obtuse to apiculate or acute, comprising ca. ¼–⅓ total length of the stamen, the internal receptacle surface with clusters of simple hairs between the stamens. Gynoecious flower in bud napiform-depressed, thick, fleshy, the size and pubescence as in the androecious bud; at anthesis urceolate-napiform, 30–40 mm diam. by 15–30 mm long, externally corky brown, sparsely puberulent, the orifice ca. 15–25 mm diam., comprising ca. ⅔ total width of the receptacle, the 6–8 thick, deltoid lobes incurved; styles very numerous, ca. 1,000–2,000, narrowly conical or setose, 1.5–5 mm long by 0.3–0.5 mm wide basally, the sides longitudinally furrowed, the internal receptacle surface densely velutinous between the styles. Fruiting receptacle solitary at the base of the trunk, irregularly cupuliform, often ± compressed dorsally, 40–85 mm long, 135–175 mm wide, the orifice subentire, 90–130 mm wide, comprising ca. ⅔–¾ total width of the receptacle, the walls 10–16 mm thick, both surfaces corky brown, internally with numerous, setose styles 1.5–4.5 mm long by 0.5–0.8 mm wide basally, the pedicel and peduncle 20–65 mm long by 9–10 mm diam. medially. Mature carpels ovoid-compressed, 10–14 mm long, 5–7 mm wide, 4–6 mm thick, the endocarp dark brown, the surface scrobiculate.

Distribution. Endemic to Mauritius (Fig. 38).

Habitat. Tambourissa ficus is fairly widespread in mid to upper elevation wet and cloud forest formations (ca. 600–800 m), often forming localized populations near the summits of mountains or along rivers and lakes.

MAURITIUS. BAMBOU MOUNTAIN: top of Bambou Mt., 7 Oct. 1962 (fl), *Mulnier sub MAU s.n.* (MAU). BASSIN BLANC: forest inside Bassin Blanc Crater, 4 Nov. 1967 (fl), *Guého sub MAU 13228* (MAU); lower montane rain forest inside crater, 550 m, 21 Dec. 1978 (fr), *Lorence 2188* (K, MAU); (fl), *Lorence 2189* (MO); (fl, fr), *Lorence 2190* (MO); ca. 2 m from outside of lake, S side, 500 m, 25 May 1976 (fr), *Richardson et al. 4164* (K, MAU, MO); indigenous forest, 13 Mar. 1971 (fr), *Staub sub MAU 19283* (MAU). BRISE FER: 200–300 yards before summit of Piton Brise Fer, 29 Dec. 1966 (fl), *Guého sub MAU 12505* (MAU, 2 sheets); (fl), *Guého sub MAU 12509* (MAU); Brise Fer Mt., 609 m, July 1960 (fr), *Lalouette sub MAU 10020* (*carpol. coll. 111*) (MAU, 2 sheets); 20 Aug. 1966 (fr), *Lalouette sub MAU 12194* (*carpol. coll. 158*) (MAU); mature evergreen forest transitional to dry forest, 600 m, 8 Dec. 1978 (fl), *Lorence 2114* (MO); (fl), *Lorence 2115* (MAU, MO); (st), *Lorence 2116* (MO); (st), *Lorence 2117* (MO); a few hundred yards before reaching the summit of Brise Fer, 1 Oct. 1964 (fr), *Vaughan sub MAU 11429* (*carpol. coll. 154*) (MAU); (st), *Vaughan sub MAU 11430* (MAU); (fl), *Vaughan sub MAU 12505* (*spirit coll. 167*) (MAU). CROWN LAND DANGUET: near Port Louis, 4 Sept. 1947 (st), *Vaughan V 3177* (MAU). MACABÉ FOREST: ravines of Black River Gorges near Macabé, 28 Nov. 1950 (fl), *Duljeet FD 105* (*spirit coll. 41*) (MAU, 2 sheets); Macabé forest, near kiosk, transitional wet forest, ca. 660 m, 16 Dec. 1978 (st), *Lorence 2155* (MAU); (st), *Lorence 2156* (MO); Plateau Colophane below Macabé, ca. 600 m, 15 Jan. 1979 (st), *Lorence 2952* (MO); Macabé, near screen, 10 Dec. 1938 (st), *Vaughan sub MAU 1336A* (MAU); Macabé forest transect, 11 Aug. 1937 (st), *Vaughan 27 sub MAU 2359* (MAU); Macabé climax forest near large "natte" tree in plot, 16 Nov. 1967 (fl), *Vaughan sub MAU 13055* (MAU). MT. COCOTTE: degraded forest, 2,200 ft. (ca. 760 m), 8 Nov. 1969 (fl), *Barclay 1692* (K); dense indigenous thicket along crest, 8 Nov. 1969 (fl), *Guého sub MAU 14108* (MAU); low cloud forest with *Nuxia,* invaded by exotics, N slope, ca. 700 m, 19 Dec. 1978 (fl), *Lorence & Lecordier 2162* (K, MO); near summit, 770 m, 19 Dec. 1978 (fl), *Lorence & Lecordier 2163* (MO, P); forest of St. Marie near Mt. Cocotte, high forest, Nov. 1937 (fl), *Wiehe sub MAU 1511* (*spirit coll. 45*) (MAU). MT DEUX MAMELLES: degraded wet forest invaded by exotics, 630 m, 22 Jan. 1979 (st), *Lorence 2303* (MO). MT LAGRAVE: low forest on slopes, much invaded, 5 Apr. 1974 (fr), *Coode 5034 sub MAU 17598* (K, MAU). PIETER BOTH MT. RANGE: S flank below "La Fenêtre," totally degraded wet forest, ca. 550 m, 29 Sept. 1978 (st), *Lorence 1833* (MO). PITON DU MILIEU: dense indigenous thicket, rocky ridge at foot of the mountain, 25 Oct. 1969 (fl), *Guého sub MAU 14181* (MAU); low native thicket halfway up steep summit, 24 Nov. 1971 (fl), *Guého sub MAU 14983* (MAU); degraded lower montane wet forest, 650–750 m, 29 Dec. 1978 (st), *Lorence 2235* (MO); (st), *Lorence 2236* (MO). PITON DU FOUGE: E slopes, ca. 500 m, 27 Apr. 1976 (st), *Richardson et al. 4042* (K). POUCE MT.: shoulder of Le Pouce, Dec. 1860 (fl), *Ayres s.n.* (K);

shoulder of Le Pouce, Nov. 1862 (fl), *Ayres s.n.* (K); (st), *Boivin s.n.* (P, mixed with *T. pedicellata*); lower montane wet forest invaded by exotics, grading into cloud forest near summit, 600–700 m, 14 Dec. 1978 (st), *Lorence 2142* (MO); (fl), *Lorence 2143* (MO); 750–800 m (fl), *Lorence 2144* (K, MAU). RIVIÈRE DES GALETS: below Cascade 500 Pieds, 350 m, forest along river bank, 8 Nov. 1975 (fl), *Lorence 1485* (K, 2 sheets; MAU); Valley of Cascade 500 Pieds, *Calophyllum* wet forest, 550 m, 22 Dec. 1978 (st), *Lorence 2193* (MO). TAMARIN FALLS RESERVES: 518 m (fl), *Vaughan sub MAU 1509* (MAU). VUILLEMAN FOREST: near Midlands (fl), *King sub MAU 1765* (MAU). WITHOUT PRECISE LOCALITY: (fl), *Anon. sub Herb. Richard s.n.* (P, 2 sheets); common in forests of medium altitude (st), *Vaughan sub MAU 1513* (MAU).

Although one of the most polymorphic Mauritian species, *Tambourissa ficus* is nevertheless distinct from all other Mascarene species, and is the only one with flowers and fruit produced on the swollen base of the trunk. It is potentially monoecious [e.g., *Wiehe 1511* (MAU), *Vaughan sub MAU 12505* (MAU), *Lorence 2162* (MAU, MO)] but frequently produces flowers of a single sex. Although only four to eight flowers are produced during a single season per plant, this paucity has been compensated for by a floral gigantism unrivalled in the genus and indeed the entire family! Fully expanded androecious flowers may attain 60–75 mm diam. with the entire surface covered by ca. 900–1,800 stamens, whereas gynoecious flowers are large, urceolate cups 30–40 mm diam. lined with a comparable number of styles. The cupuliform fruits, which attain 175 mm diam., are also some of the largest in the genus.

Both foliar and floral morphology are variable in *Tambourissa ficus,* but are relatively constant within a given population. For example, populations from the central (Le Pouce Mt., Piton du Milieu) and western (Piton Brise Fer) mountain ranges have broadly elliptic to obovate, acute to obtuse leaves, hence the specific epithet *obovata* given by Tulasne. Those from the southern edge of the central plateau (Bassin Blanc, Mt. Cocotte, Rivière des Galets) tend to have narrower, elliptic to oblanceolate, acute to acuminate leaves. Such variation may occur within a single population, however, e.g., at Macabé forest.

Variation in floral morphology is expressed in length of stamens and styles, and form and color of androecious flowers. Populations from Bassin Blanc and Rivière des Galets, which grow along river and lake banks, have shorter styles and creamy white, urceolate androecious flowers that tend to split only about halfway open. Populations from mountain summits (e.g., Le Pouce and Piton Brise Fer) have pinkish to reddish purple androecious flowers that split completely open into a star shape and the gynoecious flowers have longer styles. Flower color and size and shape of stamens and styles are similarly variable in other species, e.g., *T. tau* and *T. quadrifida.* These floral and foliar differences intergrade gradually in *T. ficus,* making it impossible to formally recognize infraspecific taxa. For example, the Bassin Blanc population has androecious flowers and styles that are transitional between the Rivière des Galets and Brise Fer forms. As such, they are best recognized as variants of a single, polymorphic species.

In view of this variation, it is not surprising that *Tambourissa ficus* has been described as three distinct species of *Ambora* by Tulasne (1855a). He based *A. obovata* on a single sterile, leafy twig from Le Pouce and based *A. alternifolia* on a mixed collection consisting of androecious buds of *T. ficus* and leaves of *Homalium* (Flacourtiaceae). Furthermore, because the type of *A. ficus* consists of leaves and gynoecious flowers of the narrow-leaved form, which moreover was supposed to have been collected in Java, it is understandable that Tulasne described it as another species. He was apparently unaware that J. Leschenault de la Tour first visited Mauritius, where he apparently collected the type of *A. ficus,* before continuing on to Java (Steenis-Kruseman, 1950). *Tambourissa* is unknown from Java, and the locality on the label is evidently erroneous (Perkins, 1911).

I have lectotypified *Tambourissa alternifolia* on the basis of the large, solitary ficiform androecious flower buds with characteristic ligulate, apiculate stamens obviously belonging to *T. ficus.* I recognize the leaves as belonging to a Mascarene species of Flacourtiaceae [*Homalium integrifolium* (Lam.) Baill.] also occurring on Le Pouce Mt. Its leafy stem is minutely lenticellate, unlike any *Tambourissa* known to me, and furthermore the leaves lack the oil cells characteristic of Monimiaceae (Perkins & Gilg, 1901), a fact ignored by Cavaco (1957b).

Baker (1877) wrongly referred material of *Tambourissa ficus* from Le Pouce to *T. elliptica.* More surprisingly, he described comparable material of the same species, also from Le Pouce, as *Ficus sapotoides,* suggesting he failed to dissect flower buds and also overlooked the absence of stipule scars on the stem. Of the three available concurrently published names, I have retained

T. ficus because the type is the most complete, with both androecious and gynoecious flowers and leaves.

Tambourissa ficus belongs to the small species Group 9, also including *T. peltata* (Mauritius) and *T. castri-delphinii* (Madagascar). The ternate to subalternate leaf condition of these species appears to be derived, as seedlings and suckers of *T. ficus* and *T. peltata* have opposite leaves. *Tambourissa ficus* is most closely allied to *T. peltata* in leaf morphology but its leaves are thinner and generally lack the bright yellow-green tinge characteristic of *T. peltata,* and the stems are more slender. In addition, *T. ficus* is monoecious, usually basally cauliflorous, and has much larger flowers with more numerous parts. Furthermore, its gynoecious flowers are urceolate with setose styles as opposed to those of *T. peltata,* which are flat and discoid with columnar styles and produce a thick, mucilaginous exudate. With respect to gynoecious floral morphology, *T. ficus* more closely approaches Group 5, thus linking the two groups.

Vernacular names. Bois tambour, Pot de chambre jacot (Mauritius).

38. Tambourissa peltata R. Br. ex Baker, Fl. Mauritius 288. 1877; Perk. & Gilg, Pflanzenr. 4, 101: 71. 1901. TYPE: Mauritius. Without precise locality, 1814, *Carmichael s.n.* (lectotype, K, here designated, as to gynoecious collection only).

Dioecious treelet or tree 12–15 m tall and 30–40 cm D.B.H., the outer bark smooth, pale brown, longitudinally fissured, the new growth glabrous, the mature leafy stems smooth, stramineate, 3–7 mm diam., angled or subterete. Adult leaves ternate to subalternate, petiolate, glabrous; petiole 12–25 mm by 1–2 mm; lamina subcoriaceous to coriaceous, broadly to narrowly obovate, oblanceolate, elliptic, broadly elliptic or rarely ovate, 60–150(–180) mm by 30–70(–85) mm (reaching 225 mm long on vigorous suckers), the apex acuminate to acute, frequently obtuse or retuse, the base acutely cuneate to acutely decurrent, the secondary veins 6–9(–12) pairs, making a 55–65° angle with the costa, the venation very prominent and finely reticulate, visible to 4° on both surfaces, the margin slightly revolute; seedling and sucker leaves opposite, heterophyllous, the petiole red when living, the lamina oblanceolate to narrowly oblanceolate, with 1–3 pairs of short teeth apically. Inflorescence ramiflorous on the leafless branches or upper portions of the trunk, rarely axillary or on short, leafy shoots, the flowers solitary or in fascicles of 2–3. Androecious flower in bud glabrous, globose to ellipsoid, 10–14 mm diam. by 12–18 mm long, apiculate with 5–6 small, acute glabrous tepals, the pedicel and peduncle 6–20 mm by 1.5–3 mm, bearing few to many deltoid-naviculate, ciliate bracteoles to 1.5 mm long; at anthesis deeply 4–6(–7)-fid, 30–50 mm diam., the thick lobes ultimately reflexing; stamens numerous, ca. 200–400, ovoid-deltoid to linear-lanceolate, 4–7 mm long by 1.5–3 mm wide, the filament short or subsessile, the loculi separate or confluent apically, occupying almost entire length of the stamen, the connective broad, slightly prolonged or not, the internal receptacle surface glabrous, rarely with scattered hairs. Gynoecious flower in bud glabrous, broadly napiform-depressed, 14–17 mm diam. by 7–9 mm long, apiculate with 4 minute tepals, the pedicel and peduncle 6–12 mm by 2 mm, bracteolate as in androecious flower; at anthesis deeply 4–7-fid, 23–30 mm diam., the deltoid lobes ultimately reflexing, their internal surface ± verrucose-wrinkled, the receptacle discoid, flat to ± concave, the peltate central portion 13–16 mm diam., pubescent around the margin and between the styles; styles numerous, ca. 400–500, crowded and coalescent, virtually indistinguishable, columnar, 4–6-sided, 0.3–0.5 mm long by 0.3–0.4 mm diam., the apex flat to depressed, the gynoecium covered with a mucilaginous exudate. Fruiting receptacle solitary on the old stems or rarely on the upper part of the trunk, sometimes produced in large numbers, cupuliform, patelliform or discoid-peltate, 40–130 mm diam. by 15–60 mm long, externally corky brown or mottled, the walls 8–20 mm thick, the orifice broad, subentire, comprising ¾ or more of the total width of the receptacle, the internal receptacle surface corky brown, with numerous short, bluntly columnar 4–6-sided styles 0.5–1 mm diam. by 0.5 mm long, often subtended by clusters of hairs, the pedicel and peduncle stout, 10–25 mm long by 6–20 mm diam. Mature carpels ovoid-compressed, 9–13 mm long, 4–8 mm wide, 3–6 mm thick, the endocarp dark brown, lustrous, the surface scrobiculate. Gametic chromosome number, $n = 19$.

Distribution. Endemic to Mauritius (Fig. 40).

Habitat. The commonest and most widely distributed species of *Tambourissa* in Mauritius,

T. peltata displays a wide ecological amplitude, ranging from lowland wet forest (e.g., at Bel Ombre, ca. 300 m, annual precipitation 2,400 mm), to upland evergreen moist forest (e.g., Mt. Corps de Garde, 750 m, annual precipitation 1,600 mm), or cloud forest (e.g., Mt. Cocotte, 760 m, annual precipitation 5,000 mm). Locally abundant in some areas, it may become a subcanopy or canopy tree (e.g., at Macabé high forest), or remain a stunted treelet (e.g., at Pétrin in *Philippia* heath formation).

MAURITIUS. BAMBOU MOUNTAIN RANGE: crest between Mt. Camisard and Piton Bambou, 28 July 1971 (fl), *Guého sub MAU 15052* (MAU). BASSIN BLANC CRATER: rain forest with *Calophyllum*, 550 m, 21 Dec. 1978 (st), *Lorence 2187* (MO). BEL OMBRE: June 1977 (fl), *Friedmann 3151* (P); wet forest with Sapotaceae, ca. 200–400 m, 27 Dec. 1978 (st), *Lorence 2213* (MO); (st), *Lorence 2214* (MO). BRISE FER MT.: Nov. 1960 (fr), *Lalouette 3008 sub MAU 10003* (*carpol. coll. 101*) (MAU). BELLE RIVE: (fr), *H. Rouillard s.n.* (MAU). CASCADE ALEXANDRA: S edge of central plateau, low, stunted wet forest, ca. 650 m, 25 Mar. 1979 (fl), *Lorence 2552* (MO). CHAMAREL HILL: top of hill, 1,100 ft. (ca. 350 m), 31 Jan. 1940 (fr), *Vaughan sub MAU 1912* (MAU, 2 sheets). CORPS DE GARDE MT.: summit ridge, ± stunted forest, ca. 750 m, 15 Nov. 1973 (fr), *Coode et al. 4064* (K, MAU). CROWN LAND RIVIÈRE: on bank along pipe to water tower, 30 July 1964 (fr), *Vaughan sub MAU 11009* (MAU). CUREPIPE: Forestry Department nursery, along stream bank with remnants of indigenous trees, ca. 700 m, 15 Dec. 1978 (fr), *Lorence 2151* (MAU, MO); 14 Mar. 1971 (fr), *Remy sub MAU 15489* (MAU). GAULETTES SERRÉES: north-central Mauritius, low mixed wet forest over lava, ca. 400–450 m, 19 May 1979 (fl), *Lorence et al. 2642* (K, MO); (fl, fr), *Lorence et al. 2643* (K, MO, P). LION MT.: by side of path leading to summit, along crest, 22 Mar. 1976 (fr), *Lalouette sub MAU 17878* (MAU). MACABÉ FOREST: Macabé to Brise Fer road, low mixed evergreen forest over laterite, ca. 660 m, 8 Dec. 1978 (fr), *Lorence 2101* (MAU, MO); Macabé forest, near kiosk, transitional wet forest, ca. 660 m, 16 Dec. 1978 (st), *Lorence 2154* (MO); Macabé forest, ca. 700 m, 7 Feb. 1975 (fr), *Lorence sub Coode 4791* (K, MAU); near path leading to Macabé via the marshes, 14 Feb. 1963 (fr), *Vaughan sub MAU 10682* (MAU, 2 sheets). MARE LONGUE PLATEAU: Mare Longue-Macabé road, on right bank of river flowing into Mare Longue reservoir, 10 Mar. 1967 (fl), *Guého sub MAU 12543* (MAU, 2 sheets); low, mixed wet forest along stream, ca. 700 m, 10 Apr. 1979 (fl), *Lorence 2586* (K, MAU, MO); 14 Apr. 1979 (fl), *Lorence 2593* (MO); near new reservoir, 1,900 ft. (ca. 600 m), 11 May 1946 (fr), *Vaughan V 3139* (*carpol. coll. 6*) (MAU, 2 sheets). MONTAGNE DES CRÉOLES: E Mauritius, transitional evergreen forest, ca. 250–300 m, 25 Jan. 1979 (st), *Lorence & Julien 2338* (MAU, MO); (fr), *Lorence & Julien 2339* (MAU, MO); (fr), *Lorence & Julien 2340* (MO); (fr), *Lorence & Julien 2341* (MO, P). PERRIER NATURE RESERVE: near Mare aux Vacoas, low mixed wet forest, ca. 600 m, 27 Mar. 1979 (fl), *Lorence 2555* (MO); 9 Apr. 1979 (fl), *Lorence 2585* (K, MO); 23 Apr. 1976 (fr), *Richardson et al. 4009* (K, MAU); (fr), *Richardson et al. 4010* (K); near quadrat by small stream, Dec. 1937 (fl), *Vaughan sub MAU 1437* (MAU, 2 sheets); (fl), *Vaughan sub MAU 1438* (MAU); 15 June 1939 (fl), *Vaughan sub MAU 1534* (MAU); 6 June 1969 (fl), *Vaughan sub MAU 13774* (MAU, 2 sheets); in dense indigenous thicket, 14 May 1970 (fl), *Vaughan sub MAU 14184* (MAU); (fl), *Vaughan sub MAU 14185* (MAU, 2 sheets); 22 Apr. 1970 (fl), *Vaughan sub MAU 14193* (MAU, 2 sheets); by stream, 9 Oct. 1975 (fr), *Vaughan sub MAU 17543* (MAU). PÉTRIN NATURE RESERVE: *Philippia* heath formation over laterite, 630 m, 4 Apr. 1979 (fl), *Lorence 2572* (MO, P). PIETER BOTH MT.: S flank below La Fenêtre, very degraded wet forest invaded by exotics, ca. 400 m, 23 Jan. 1979 (st), *Lorence 2319* (MAU, MO). PLAINE CHAMPAGNE: road to Plaine Champagne, dense indigenous thicket, 21 July 1966 (fr), *Guého sub MAU 12232* (MAU, 2 sheets); SE of triangulation point, low heath formation of *Philippia* and *Helichrysum* over laterite, ca. 700 m (fr), *Lorence 2197* (MAU, MO). POUCE MT.: Le Pouce Mt. plateau, mixed wet forest invaded by exotics, grading into cloud forest near summit, 600–700 m, 14 Dec. 1978 (fr), *Lorence 2146* (K, MO); 14 Feb. 1979 (fr), *Lorence 2402* (B, K, MAU, MO, P, REU, Z). SEPT CASCADES: (fr), *Hardy s.n.* (MAU). TAMARIN RIVER: river reserves near Tamarin River Bridge, at Mare aux Vacoas, 2 June 1966 (fl), *Vaughan sub MAU 12168* (MAU, 2 sheets); 5 May 1966 (fl), *Vaughan sub MAU 12240* (MAU, 2 sheets). VACOAS RIDGES: 21 Jan. 1968 (fr), *Guého sub MAU 13077* (*carpol. coll. 175*) (MAU). WITHOUT PRECISE LOCALITY: (fr), *Anon. sub MAU 11004* (*carpol. coll. 159*) (MAU); (fl), *Anon. 3132* (G); (st), *Bojer sub MAU 1312* (MAU); (fl), *Carmichael s.n.* (K, syntype); (st), *Carmichael s.n.* (K); (fr), *Remy s.n.* (MAU); 16 Aug. 1962 (fr), *Tilbrook sub MAU 10548* (MAU); 3 Sept. 1962 (fr), *d'Unienville sub MAU 10624* (MAU); 30 Mar. 1964 (fl), *d'Unienville sub MAU 11206* (MAU, 2 sheets).

Leaf shape in *Tambourissa peltata* is relatively variable, a character which tends to remain constant within populations. Populations from the eastern mountain ranges (e.g., Montagne des Créoles, Mt. de Lion, and Mt. Bambous) are characterized by narrowly elliptic to oblanceolate leaves, whereas most populations from the upland plateau have the usual obovate leaves. Fruit morphology ranges from typically cupuliform to flat and discoid, both extremes occasionally on the same tree (e.g., *Lorence 2151*). Androecious flower size and color are variable within populations but remain constant on a given tree. Dark purple-red androecious flowers are most common, whereas the salmon pink ones are less frequent. Gynoecious flower color is less variable, the central disc being reddish orange and the sterile lobes dull purple-red and verrucose. At anthesis, the disc secretes a copious thick, clear mucilage which covers the styles and is probably functional in pollination (see Endress,

1979, 1980b). Flowers of both sexes produce strong, sour odors of fermenting fruit or tomatoes.

Tambourissa peltata belongs to the small species Group 9, whose members are characterized by ternate to subalternate leaves, also including *T. ficus* (Mauritius) and *T. castri-delphinii* (Madagascar). *Tambourissa peltata* strongly resembles and is apparently closely related to the latter species; both are ramiflorous with similar androecious flowers and stamens, and have leaves with prominent, finely reticulate venation. *Tambourissa peltata* differs by its larger, solitary or fasciculate androecious flowers and is the only species known to have flat, discoid gynoecious flowers with star-like sterile lobes. Flowers of *T. ficus* are much larger than those of the preceding species and are produced at the swollen base of the trunk. The only other dioecious species in Mauritius, *T. cordifolia,* does not seem to be closely related to *T. peltata,* but rather belongs to species Group 5, although the two are known to hybridize naturally at Pétrin.

Vernacular name. Bois tambour (Mauritius).

IMPERFECTLY KNOWN SPECIES

39. Tambourissa lastelliana (Baill.) Drake in Grandidier, Hist. Phys. Madagascar 1(1): 24. 1902; Perk., Pflanzenr. 4, 101 (Nachtr.): 44. 1911. *Monimia lastelliana* Baill., Bull. Mens. Soc. Linn. Paris 1: 342. 1882; Perk. & Gilg, Pflanzenr. 4, 101: 65. 1901. TYPE: Madagascar. Without precise locality, 1841, *de Lastelle s.n.* (holotype, P).

Dioecious (?) shrub or tree (?), the mature leafy stem glabrous, 4 mm diam., longitudinally striate-pustular, the rays relatively narrow, the nodes dilated, with multiple axillary buds, the internode 80 mm long. Leaves opposite, petiolate; petiole recurved, 15 mm by 2 mm, glabrescent; lamina thickly chartaceous, brown, adaxially glabrescent, abaxially with scattered simple, straight to slightly curved simple hairs 0.5 mm long, denser and longer (to 1–1.5 mm) along the major veins and costa, the lamina broadly obovate-cuneate, ± involute, the apex shortly acuminate, the base cuneate, the apical portion of the lamina with 4–5 pairs of broad, deltoid teeth 1.5–4 mm long, the tips indurated, the venation mixed, basally festooned brochidodromous, apically craspedodromous, the secondary veins excurrent into the marginal teeth, ca. 5 pairs, making a 35–40° angle with the costa, the venation strongly depressed adaxially and visible to 3°, raised abaxially and visible to 4°, the margin revolute. Androecious inflorescence ramiflorous (?), presumably a dichasium or the flowers solitary, the floral axis pilose-tomentose basally, fulvous, ca. 10 mm by 1.5 mm or longer, subtended by several obtuse-deltoid tomentose bracteoles. Submature androecious flower in bud 6–7 mm diam., globose, densely golden pilose externally, the apex slightly depressed, with several minute tepals, the pedicel ca. 5 mm by 1 mm, golden pilose; stamens ca. 60–70 per flower, in bud ca. 3–4 mm long by 1 mm wide, the loculi lateral, separate, occupying the medial ⅔ of the stamen, laterally dehiscent, the filament short, the connective prolonged, acute, the internal receptacle surface with scattered simple hairs between the stamens; tanniferous idioblasts and oil cells present in the receptacle wall.

Distribution. Presumably endemic to Madagascar. The type is said to be from eastern Madagascar (Baillon, 1882), presumably from low or mid altitude evergreen wet forest.

The type of *Monimia lastelliana* consists of a single, detached leaf, a leafless twig, and several detached androecious flower buds. Unlike *Monimia,* which has entire leaves with festooned brochidodromous venation and predominantly or uniquely stellate trichomes, the leaf of *de Lastelle s.n.* has dentate margins in the apical portion, mixed craspedodromous and brochidodromous venation, and bears only simple trichomes as do the flower buds. Furthermore, stamens of *de Lastelle s.n.* lack the paired basal appendages characteristic of *Monimia* and have instead long, laterally dehiscent loculi and an acutely prolonged connective, all lacking in *Monimia* as noted by Perkins (1911). The pollen is too immature to permit diagnosis. Nevertheless, it is clear that *de Lastelle s.n.* does not represent a species of *Monimia,* nor even belong in the subfamily Monimioideae (sensu Thorne, 1974), and was correctly removed from the genus by Drake del Castillo (1902).

Its eglandular stamens with laterally dehiscent loculi, and long, uniquely simple trichomes instead suggest placement in the subfamily Mollinedioideae (sensu Thorne, 1974) with the other Madagascan genera. The globose buds with minute, reduced tepals most closely recall those of

Tambourissa. Although venation is festooned brochidodromous in most *Tambourissa* species, that of *T. longicarpa* and *T. thouvenotii* is basally brochidodromous and tends to become craspedodromous in the toothed apical portion of the lamina, much as in *de Lastelle s.n.* On the basis of androecious floral morphology and leaf structure, it is most probable that *de Lastelle s.n.* actually does represent a species of *Tambourissa* as proposed by Drake del Castillo (1902).

40. Tambourissa sp. A.

Habit unknown. Leaves opposite, petiolate; petiole 17–24 mm long; lamina chartaceous, elliptic, 80–100 mm by 34–43 mm, the apex acuminate, the base cuneate, the venation visible to 5–6° on both surfaces. Androecious inflorescence (cauliflorous?) a dichasium, the elongate floral axis ca. 130 mm long; the androecious flower in bud cylindrical, obovoid-ellipsoid, ca. 12–15 mm long, apiculate, the pedicel 7 mm by 1 mm; at anthesis splitting deeply into 3 segments; stamens numerous, ligulate, ca. 2 mm long, the loculi confluent apically, occupying nearly the entire length of the stamen; flowers red when living. Gynoecious flowers, gynoecious inflorescence, and fruit unknown.

MADAGASCAR. TAMATAVE: Iaroka, Maroantsetra, 1,000 m, 20 June 1968 (fl), *Rakotozafy 847 bis* (MAD).

The elongate androecious buds most closely resemble those of *Tambourissa quadrifida* from Mauritius. It probably represents an undescribed species from the mid altitude *Tambourissa/Weinmannia* wet forest zone.

41. Tambourissa sp. B.

These collections have opposite leaves, the petiole to 23 mm long; lamina coriaceous, obovate, to 85 mm by 48 mm, the apex obtuse, emarginate, the base cuneate, the margin revolute. Immature androecious flower buds ramiflorous on leafless nodes, solitary, the pedicel ca. 20 mm long, the bud 7–8 mm diam., the stamens with lateral loculi and a prolonged connective.

MADAGASCAR. FIANARANTSOA: Ampamaherana, 14 Dec. 1949 (fl), *Anon. sub SF-1252* (MAD, P).

The species resembles *Tambourissa crassa* from Réunion in leaf, but in the latter species the flowers are larger and always terminal, and the connectives are not prolonged. This collection probably represents an undescribed species for which I could not find the precise locality on any map.

42. Tambourissa sp. C.

Tambourissa amplifolia sensu Cavaco in Humbert, Fl. Madagascar 80: 34. 1959 non (Bojer ex Tul.) A.DC.

Tree to 5 m, the leaves large, the petiole 10–16 mm long, the lamina ovate-elliptic, 140–180 mm by 60–80 mm, shortly acuminate apically, rounded basally, the secondary veins 4–7 pairs. Unlike *Tambourissa amplifolia* (Mauritius), the petioles, costa, and veins are densely hirtellous abaxially.

MADAGASCAR. FIANARANTSOA: Farafangana, Befotaka, 17 Aug. 1926 (st), *Decary 5040* (MAD, P); NE Madagascar, without precise locality (st), *Thiny s.n. in 1904* (P).

These collections either represent an undescribed species from the lowland wet forest zone in the northeast and east, or may be referable to *T. decaryana*, for which only inflorescence leaves are known.

43. Tambourissa sp. D.

Habit unknown. Leafy stems pale brown, velutinous, 1.5–2 mm diam., the new growth velutinous. Leaves opposite, petiolate; petioles 5–10 mm by 1 mm, velutinous; lamina subcoriaceous, adaxially glabrescent, abaxially pubescent, especially along the costa and major veins, ovate-elliptic, the apex acute to shortly acuminate, the base acutely cuneate, slightly decurrent, the secondary veins 4–6 pairs, making a 55–60° angle with the costa, the venation visible to 2(–3°) adaxially, to 4° abaxially, the margin entire, revolute. Flowers unknown. Fruiting receptacle (fide Baron's pencil sketch of *6720*, K) terminal, subglobose, ca. 45–55 mm diam., the orifice subcircular, subentire, comprising ca. ¼–⅓ total width of the fruit. Mature carpels unknown.

MADAGASCAR. N Madagascar (probably DIEGO SUAREZ): without precise locality, ca. 1882 (st), *Baron 6720* (K; see also Baron's sketch of a fruit with the specimen).

Distribution. Presumably endemic to Madagascar.

The collection consists of two sterile leafy branches plus Baron's pencil sketch of the fruit. The leaves are similar to those of *Tambourissa sieberi* (Mauritius), but differ in having numerous oil cells dispersed throughout the laminar tissue and in having less highly branched venation (only to 4°), nor does *T. sieberi* ever have solitary, terminal fruits. It probably represents an undescribed species.

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MOSSES (1)—FLORA OF SOUTHERN AFRICA. R. E. Magill. xv + 291 pp. 1982. $30.00.

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MOSSES OF EASTERN NORTH AMERICA. H. A. Crum & L. E. Anderson. 2 vols. 1328 pp. Illustrated. 1981. $75.00.

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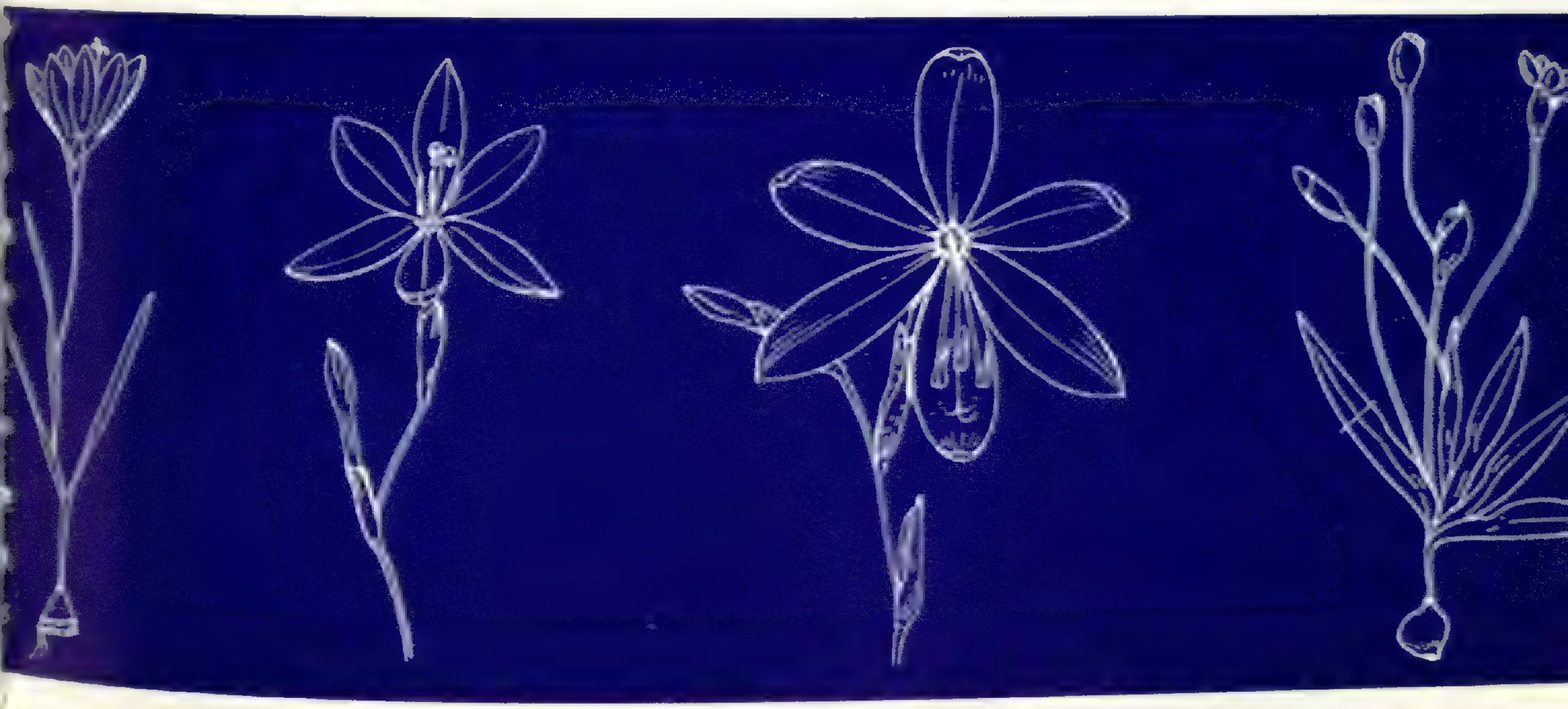

Geissorhiza

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FAMILIAL POSITION OF THE CAPE GENUS *EMPLEURIDIUM*[1]

PETER GOLDBLATT,[2] HIROSHI TOBE,[3] SHERWIN CARLQUIST,[4]
AND VARSHA C. PATEL[5]

ABSTRACT

The monotypic southwestern Cape genus *Empleuridium* was assigned with doubt to Rutaceae when first described in 1860. Poorly known until recently, it has been rediscovered and new collections have made possible detailed studies of its embryology and reproductive anatomy; stem and leaf anatomy; and pollen. Results confirm that *Empleuridium* is misplaced in Rutaceae and it seems best referred to Celastraceae, in which it is unusual in its ericoid habit, small size, and unilocular ovary that develops into a follicle-like single-seeded fruit. The very small flowers have a floral disc in which the inferior ovary is embedded. Previous observations that *Empleuridium* was dioecious are incorrect; the flowers are perfect.

The monotypic genus *Empleuridium* was first described in 1860 and was based on a collection made by the early Cape collectors Ecklon and Zeyher in the 1820s. Publication was nearly simultaneous in "Flora Capensis" (Sonder, 1860) and in a series of illustrations, the "Thesaurus Capensis," intended to supplement the Flora (Harvey, 1859–1860). *Empleuridium* is usually attributed to Sonder, and the species *E. juniperinum* to Sonder & Harvey. It was assigned with doubt to Rutaceae by Sonder and has since remained in this family in generic floras of Southern Africa (Phillips, 1926, 1951; Dyer, 1975).

Empleuridium is a small shrub with needle-like leaves and small tetramerous flowers, the four stamens located at the edge of a floral disc and alternating with the petals. It is rare and apparently had not been recollected for over 120 years when Elsie Esterhuysen, the well known Cape botanist who has made a study of the Cape mountain flora, found plants growing on rocky mountain slopes at two localities in the southwestern Cape. She realized that her find was unusual and collected ample material, including a supply of specimens fixed in FAA. Subsequently, the first author suggested to her that the plants in question might be the poorly known *Empleuridium*. An examination of the type material at Stockholm (S), made by the Director, Dr. B. Nordenstam, confirmed this.

[1] Supported in part by Grant DEB 81-19225 from the United States National Science Foundation. We thank Elsie Esterhuysen, University of Cape Town, for freely making available her collections of *Empleuridium* for our study and for assisting in the collection of more material, together with Mike Viviers, South African Department of Forestry. We also thank Peter Raven for encouraging this study and for bringing the authors together, and Rolf Dahlgren, Botanical Museum, Copenhagen, for reviewing the manuscript.

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Empleuridium apparently does not belong in Rutaceae according to Dr. I. Williams (pers. comm.), who has revised several southern African genera of this family, including *Empleurum*, to which *Empleuridium* is superficially similar. Because the affinities of *Empleuridium* are not known, this study was undertaken in the hope of establishing more satisfactorily the relationships of the genus. Embryological and floral anatomy studies were made by Hiroshi Tobe; stem and leaf anatomy by Sherwin Carlquist; and pollen by Varsha Patel.

MATERIALS AND METHODS

Plants used in this study were collected in the wild and preserved in FAA. Voucher data is as follows: *Empleuridium juniperinum* Sonder & Harvey:

South Africa: Cape, Caledon district, above De Rust, 3,000 ft., *Esterhuysen 34318* (BOL, MO, RSA).

South Africa: Cape, Caledon district, upper slopes of Mt. Lebanon, 3,800 ft., *Goldblatt 6918* (MO).

Wood studies were supplemented with herbarium material of a portion of root (*Esterhuysen 34318*-RSA).

EMBRYOLOGY

For light-microscopic observations, FAA preserved flowers and fruits at various stages of development were dehydrated through a *t*-butyl alcohol series and embedded in Paraplast with a melting point of 56–58°C. Serial sections cut 5–10 μm thick were stained with Heidenhain's hematoxylin, safranin and fastgreen FCF, and were mounted in Canada Balsam. Electron-microscopic observations on seeds were also made following a standard technique and using JSM-25S (JEOL).

VEGETATIVE ANATOMY

Dried root material was boiled preparatory to further treatment. Prior to sectioning, both the FAA and dry material were treated in ethylene diamine for softening in preparation for paraffin sectioning, a technique (Carlquist, 1982) in which small twigs or objects with both hard and soft portions can be sectioned successfully. A safranin-fast green combination was used for staining sections. Macerations were prepared with the aid of Jeffrey's fluid.

POLLEN

Buds containing pollen were treated by acetolysis (Erdtman, 1960), air dried from 95% ethanol, sputter coated with gold, and examined with an International Scientific Instruments Super II scanning electron microscope. Slides of glycerine jelly mounts were also examined with transmitted light using a Leitz Ortholux microscope.

OBSERVATIONS

FLORAL MORPHOLOGY

The flowers are solitary and borne in the axils of the needle-like leaves. The pedicels are 1.5–2 mm long at flowering, elongating up to 3 mm in fruit (Fig. 4). A pair of tiny opposed scaly bracts (Fig. 4) are present at the base of the pedicel. The flowers are small, 1.5–2 mm long and ca. 2 mm in diam.; perfect and tetramerous, comprising four sepals and four petals apparently arranged in whorls, but decussate in young buds (Fig. 2). There are four stamens and an ovary (Figs. 2, 3; see also Fig. 6) of probably four carpels (see next section). The stamens are alternate with the petals (Fig. 2), i.e., haplostemonous. Aestivation of the sepals and petals is imbricate (Fig. 2). The filaments are short, ca. 1 mm long. A style is also very short with a capitate stigma (Fig. 4). A nonnectariferous disc is slightly developed in the intrastaminal area. Both the sepals and the style are persistent.

The ovary is hemi-inferior and embedded in the receptacle (Fig. 1; see also Fig. 6A, B). The ovary is unilocular with four (occasionally three) erect ovules, and completely lacks the septa (Figs. 1, 3) that would represent the fused lateral walls

→

FIGURES 1–5. Morphology and anatomy of flower and fruit of *Empleuridium*. se, sepal; pe, petal; st, stamen; ov, ovule; sc, scaly bract; pd, pedicel; fr, fruit coat; sd, seed.—1. Longitudinal section of a flower bud. Scale = 200 μm.—2. Transverse section (TS) of a flower bud at the level of anther. Note imbricate aestivation of sepals and petals. Scale = 100 μm.—3. TS of a flower bud at ovary level. Note the ovary is unilocular and occasionally contains only three ovules. Scale = 200 μm.—4. Fruit in various stages of development. The one on the right is nearly mature. Scale = 2 mm.—5. TS of a young fruit: the fruit is one-seeded and the fruit coat has no secretory cavities. Scale = 200 μm.

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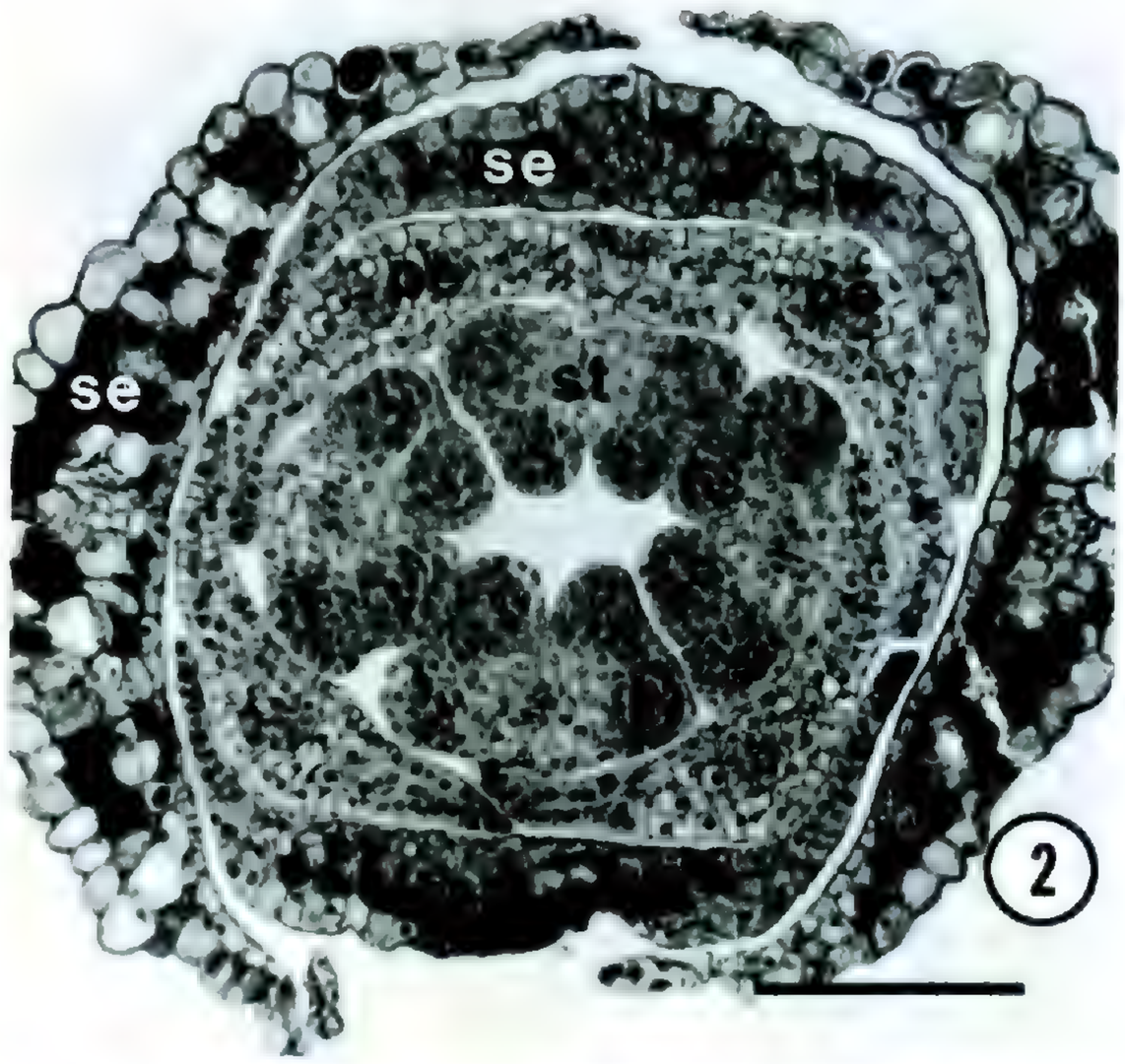

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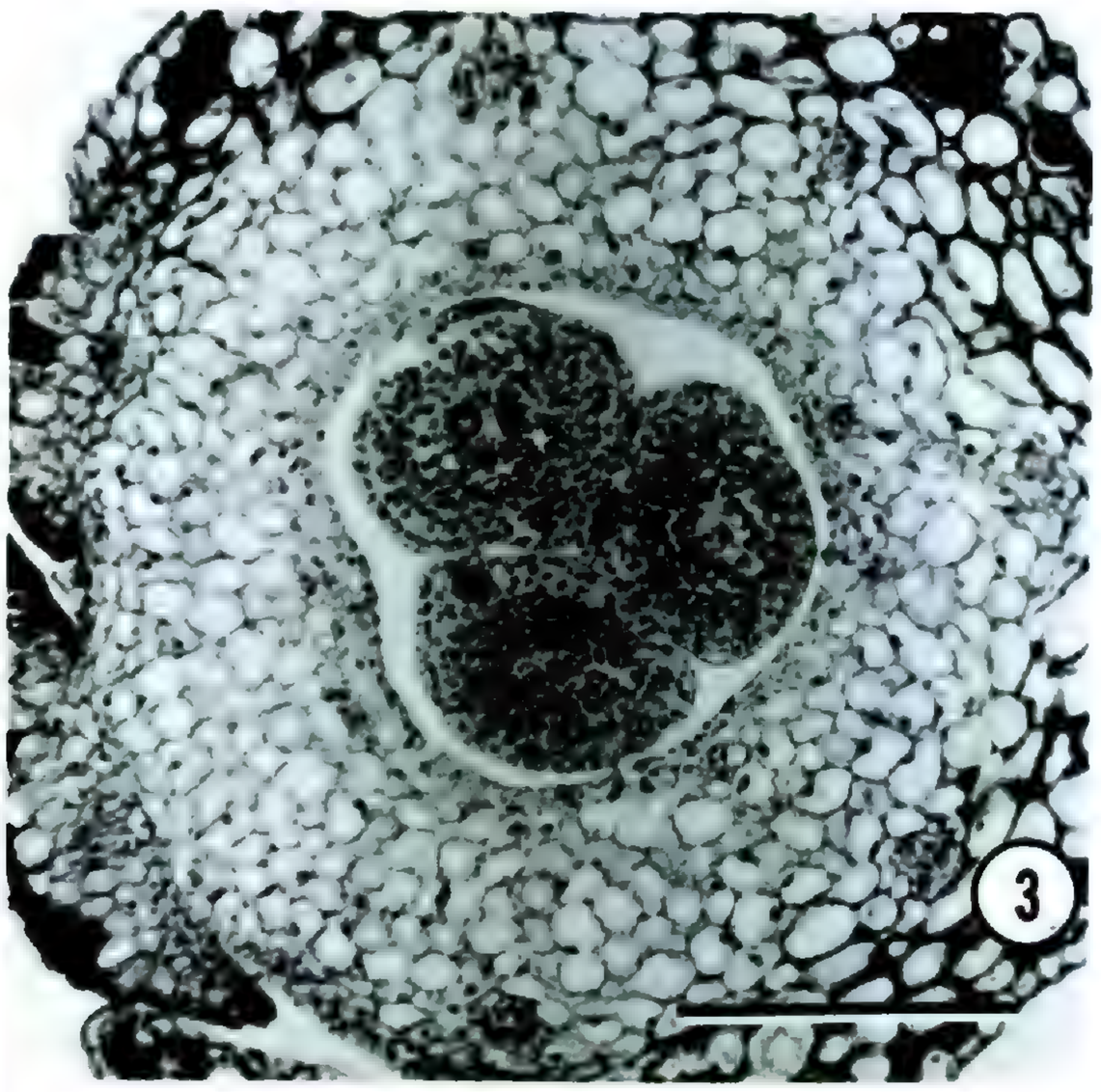

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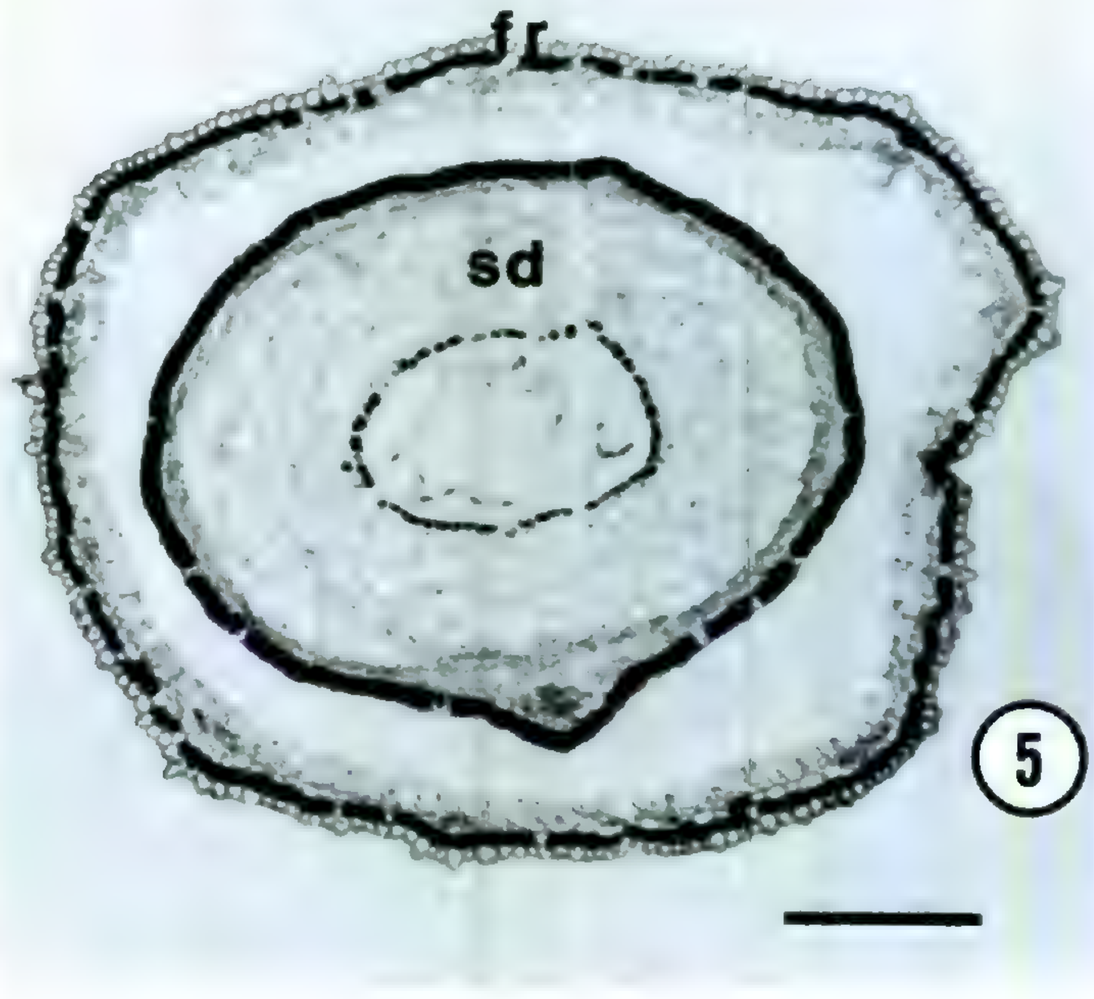

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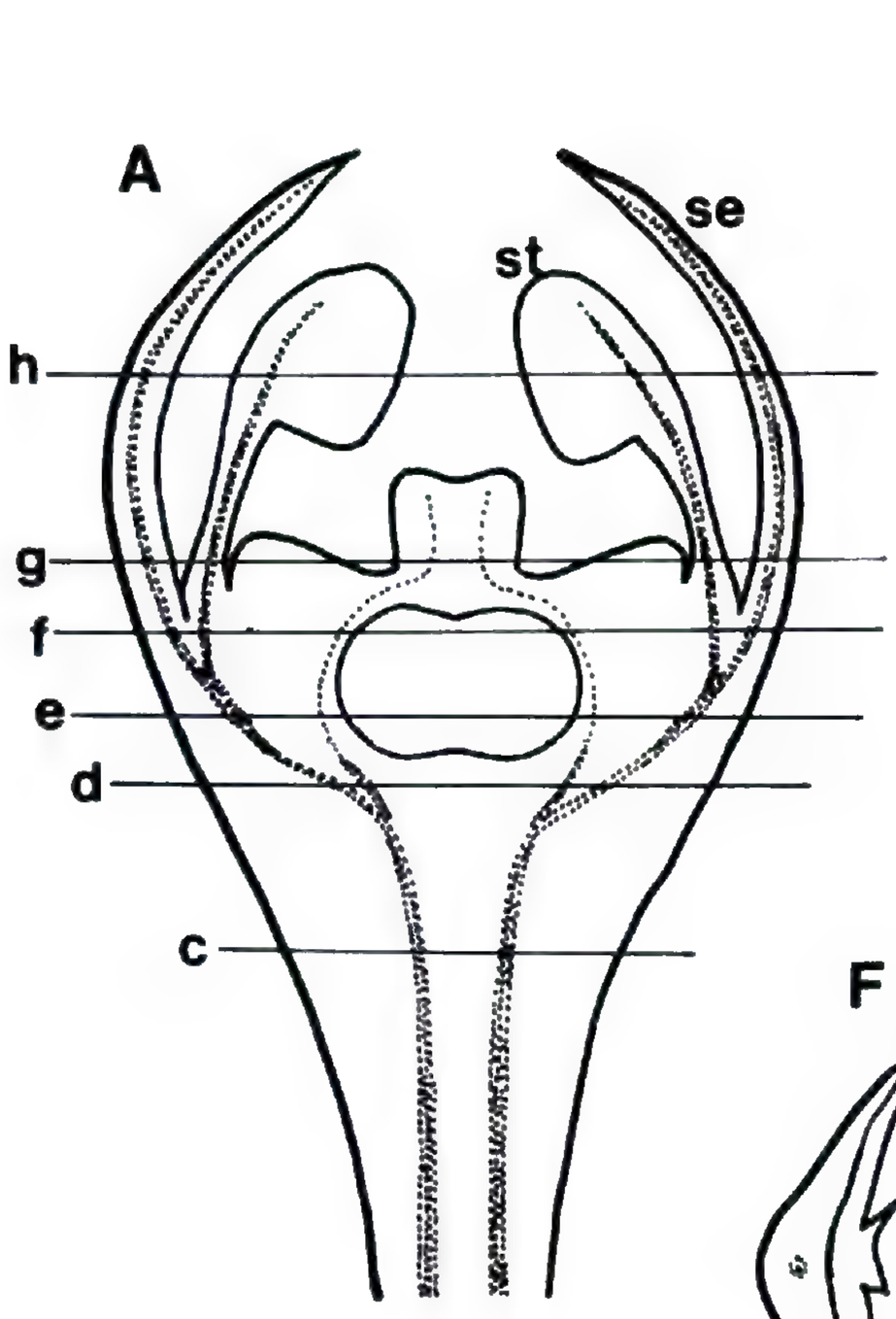
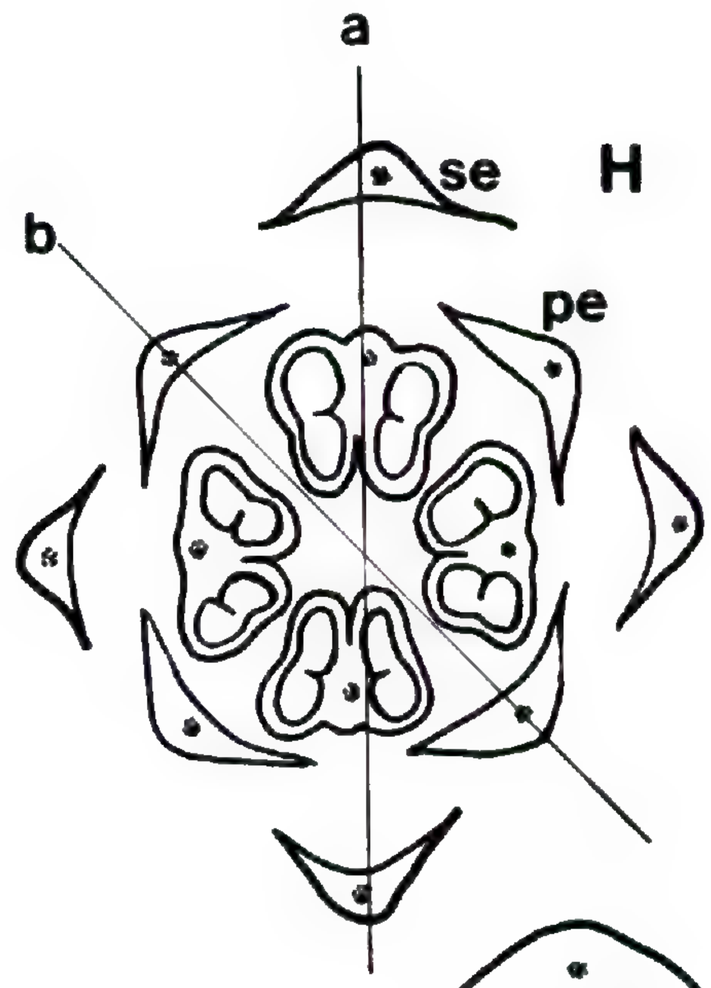
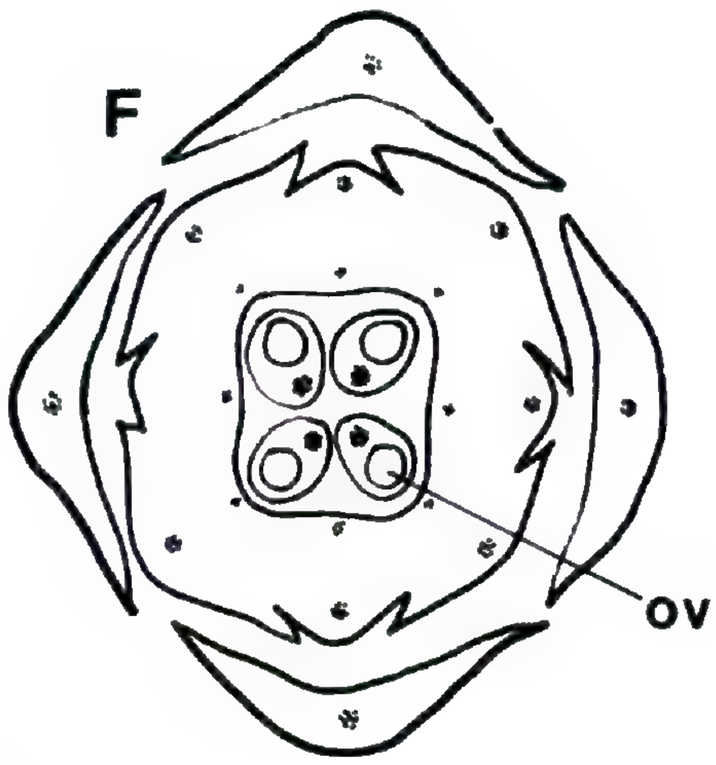
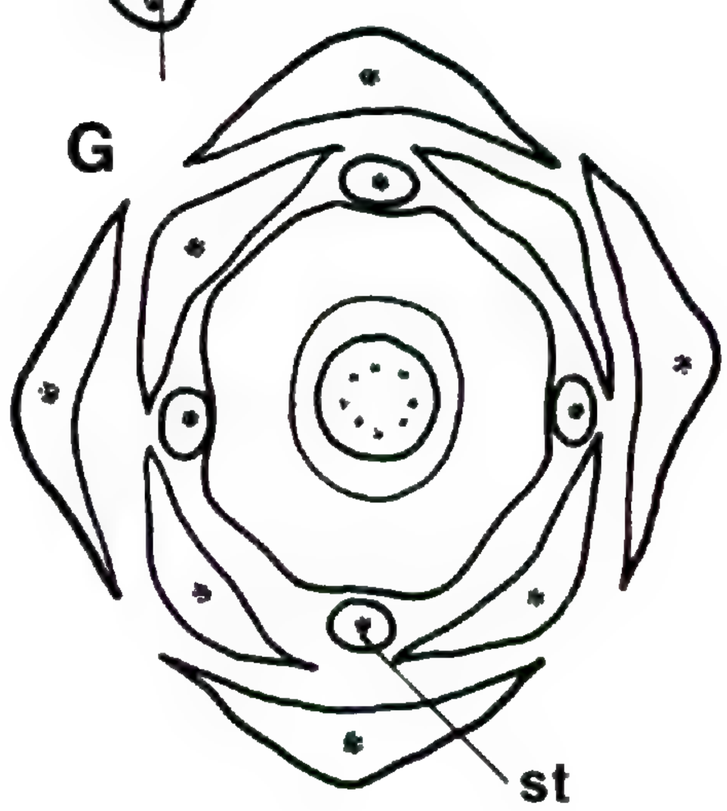
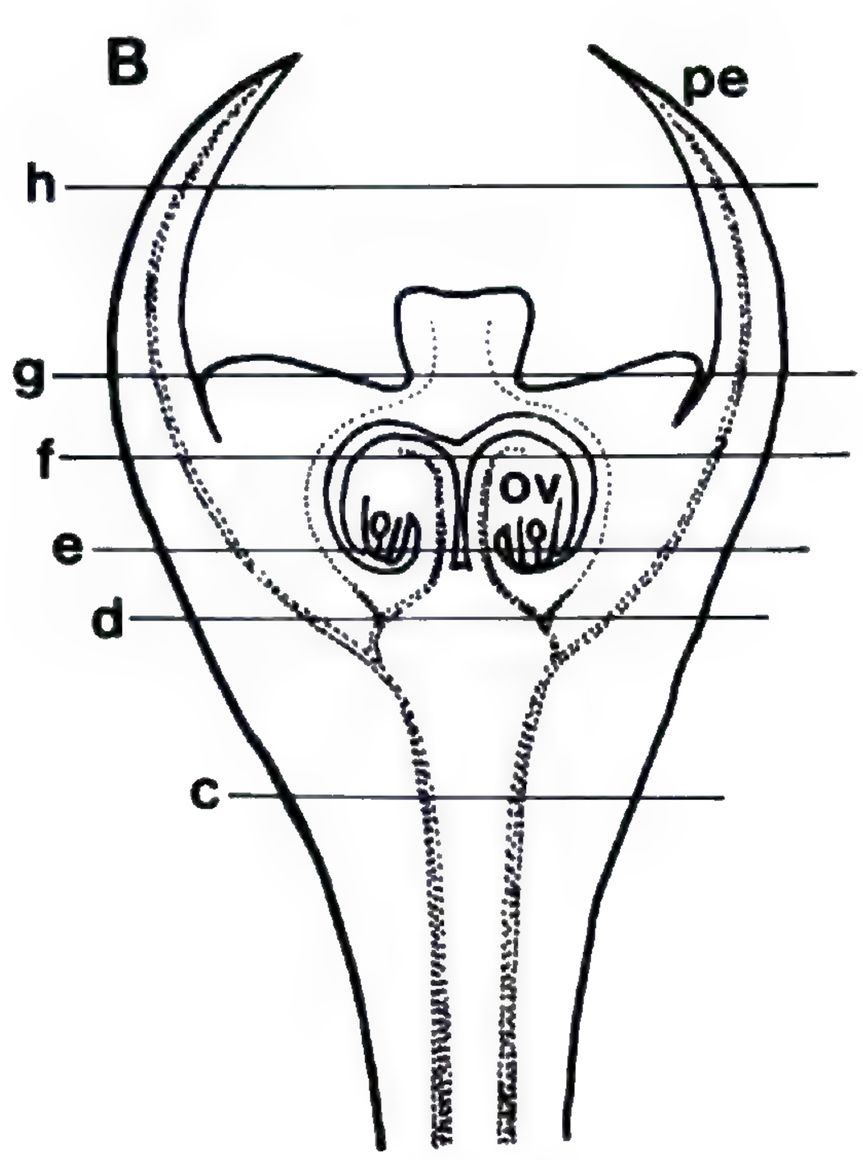
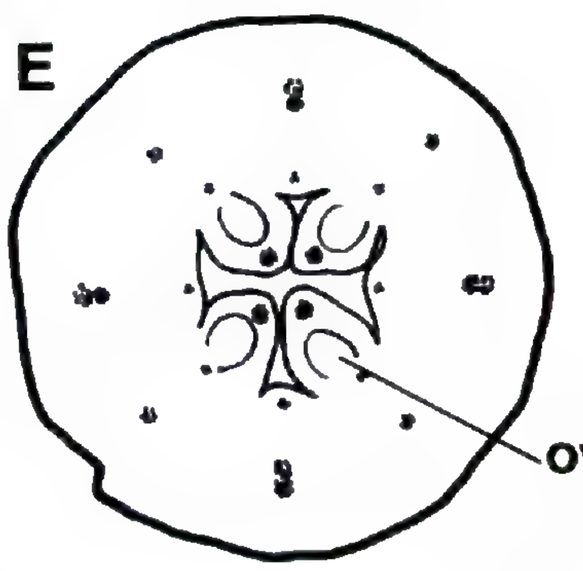


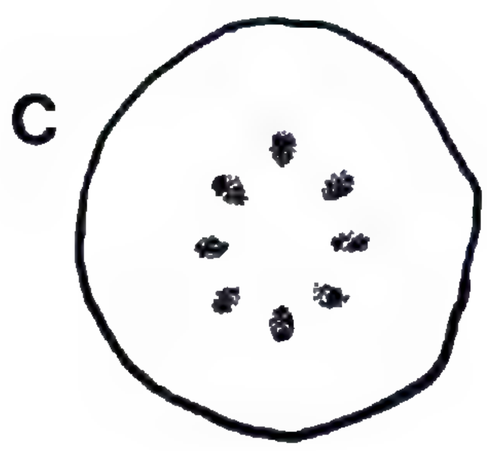












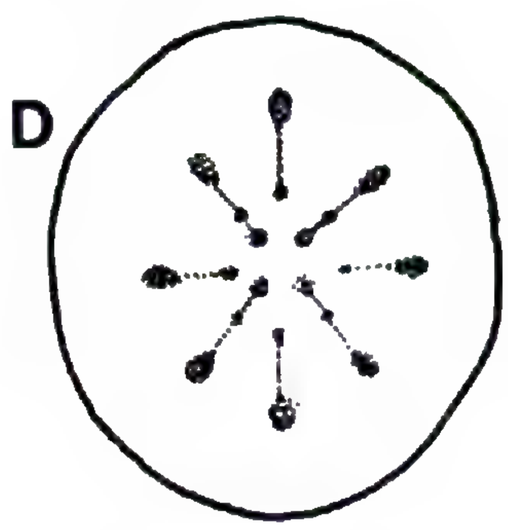


FIGURE 6. Diagrams illustrating the floral anatomy and vasculature in *Empleuridium*. Symbols are the same as those in Figures 1–5.—A, B. Median longitudinal sections of a flower through the line marked a and b in H.—C–H. Transverse sections of a flower at levels marked c–h in A and B.

of the constituent carpels. The ovules are alternate to the stamens (see Fig. 6F). Placentation is basal (Figs. 1, 6B).

Although the ovary is initially inferior, it elongates beyond the level of the stamens after fertilization (Fig. 4). At maturity all but a tiny part of the fruit extends beyond the receptacle. The fruit is 7–9 mm long, fusiform and slightly curved with a tapering persistent style. It is always one-seeded (Fig. 5) and is follicle-like, although strictly a capsule since it is derived from a compound ovary. The fruit wall is thin and consists of four to five cell layers and lacks secretory cavities expected in Rutaceae. The large, black seed has a distinctive white aril or elaiosome at the base which has several thread-like coiled extensions. This is described in more detail in a later section.

FLORAL ANATOMY

Vasculature of the flower is very simple, and does not form a network by mutual fusions of vascular bundles in the receptacle. At the basal part of the receptacle there are eight discrete (collateral) bundles (Fig. 6C), each supplying the vascular traces to either a sepal/stamen or a petal/particular ovary-wall part/ovule, depending on the dispositional relationship between the vascular bundle and appendages (Fig. 6D–H). The sepals, petals, and stamens each have a single bundle (Fig. 6H). In the wall of the inferior ovary there are eight small vascular bundles that extend upward into a short style (Fig. 6E, G). Vascular strands entering the four ovules are separately derived from the four vascular bundles, which are opposite the four petals respectively, and each of which emits traces not only to a petal but also to the dorsal part of the ovary wall.

The vascular anatomy suggests that the four ovules in the single ovary are originally those of four carpels. It seems that the unilocular hemi-inferior ovary of *Empleuridium*, containing four ovules evolved from a four-carpellate, septate compound ovary by loss of septa.

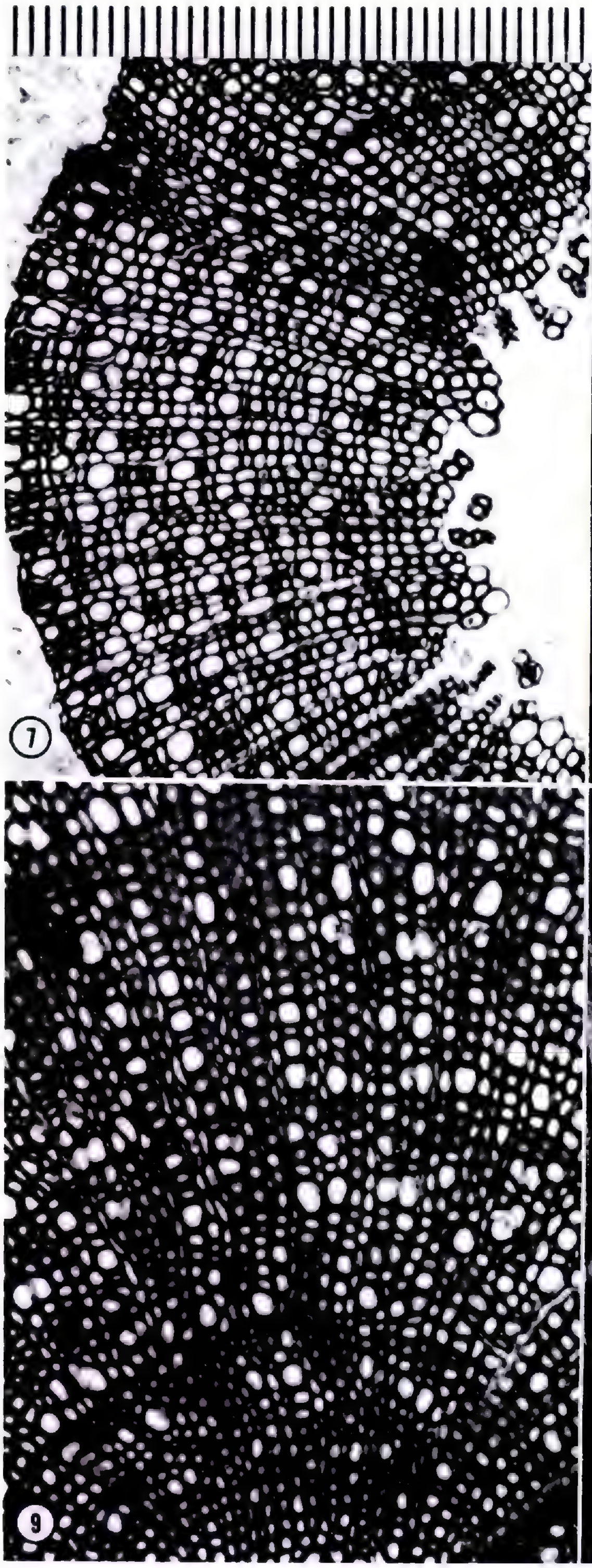
VEGETATIVE ANATOMY

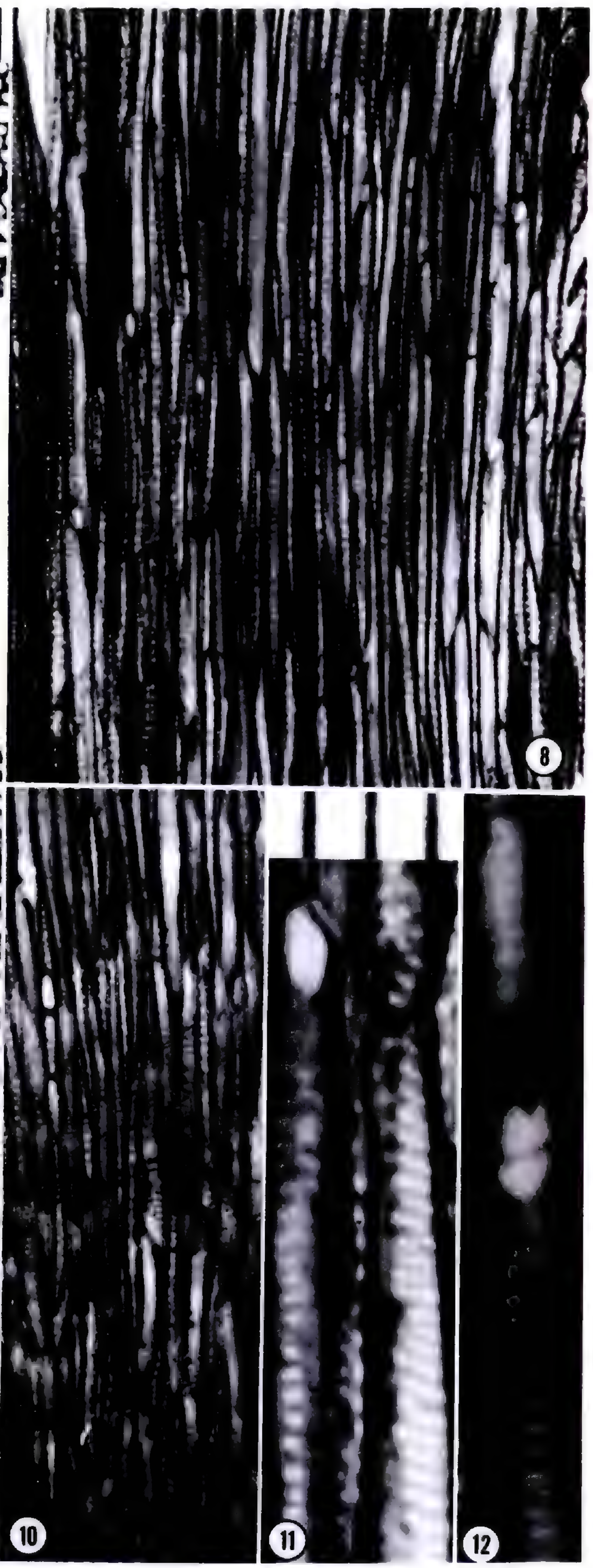
Wood (Figs. 7–12). Wood of stems (Figs. 7, 8) is described first here; features by which root wood differs follow. Stem wood with occasional vague growth rings demarcated by wider vessels in earlywood. Vessels are angular to rounded in transectional view; mean vessel diam., 15 μm; mean vessel wall thickness, 1.4 μm. Mean number of vessels per sq. mm is 844. Mean vessel element length, 136 μm. Perforation plates simple, a few with a transverse bar. Lateral walls of vessels with alternate or scalariform pitting. Imperforate tracheary elements all tracheids with fully bordered pits. Mean tracheid wall thickness, 3 μm; mean tracheid length, 282 μm. Axial parenchyma sparse, vasicentric (because of vessel abundance, contact of axial parenchyma is virtually inevitable), axial parenchyma in strands of two cells. Rays few, uniseriate, all composed of markedly erect cells; the wood appears nearly rayless (Fig. 8). Wood non-storied.

Wood of root like that of stem except for the following features. Root wood with little growth ring activity (Fig. 9). Mean vessel diam., 25 μm; mean vessel wall thickness, 2.5 μm. Mean number of vessels per sq. mm is 494. Mean vessel element length, 316 μm. Perforation plates simple (Fig. 11) or with one to three bars (Fig. 12). Lateral walls of vessels with alternate pits or pits which may be provisionally termed scalariform (Fig. 11). Mean wall thickness of tracheids, 4.6 μm; mean tracheid length, 520 μm. Wood nearly rayless (Fig. 10), an occasional uniseriate ray composed of erect cells present.

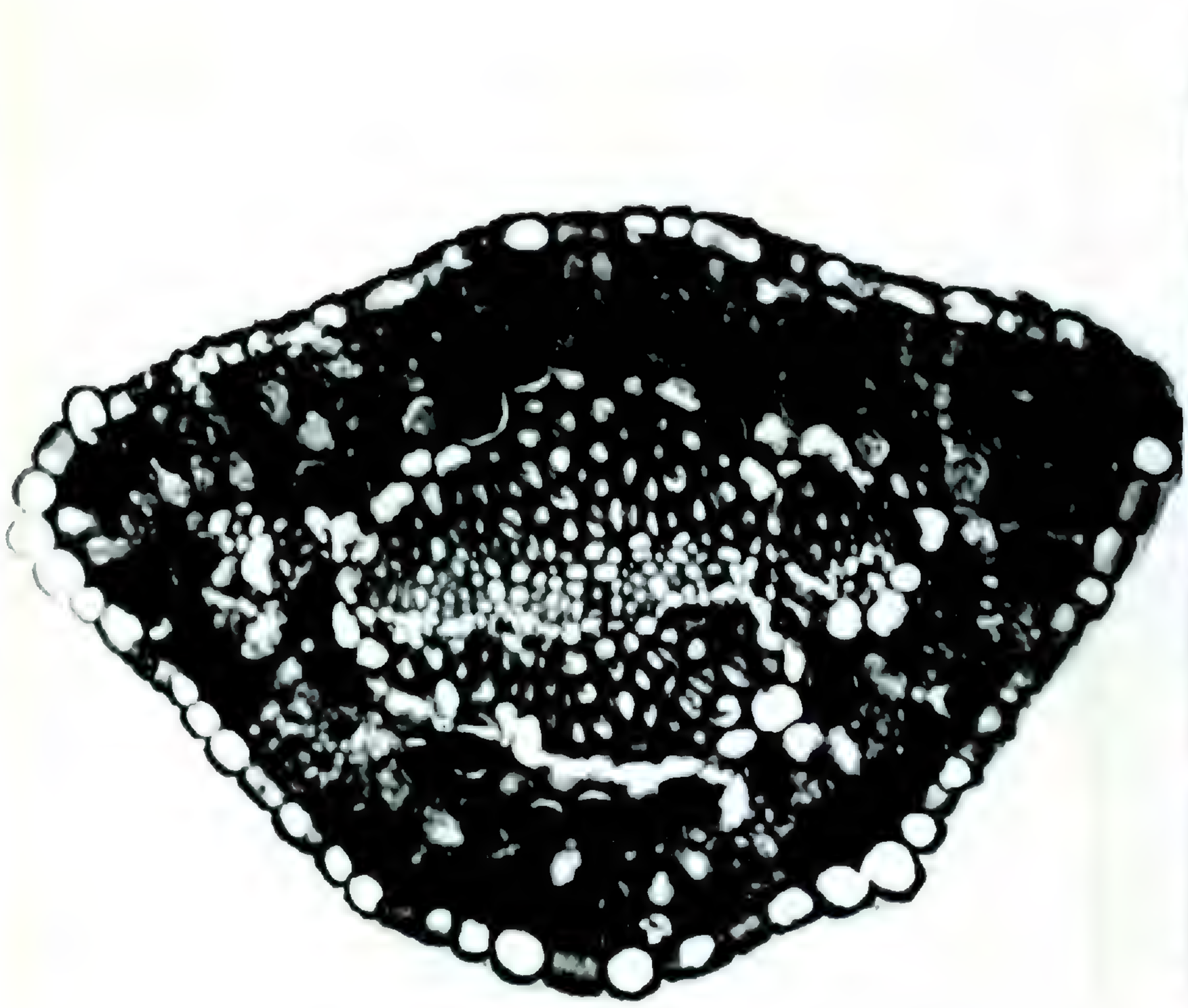
Node, cortex, and phloem. Nodes of *Empleuridium juniperinum* are all unilacunar with a single trace. The cortex is composed wholly of parenchyma cells except for a few scattered protophloem fibers in stems; fibers absent in roots (Fig. 15). Scattered tannin-bearing idioblasts and druse-bearing idioblasts present in both roots and stems (Fig. 15). Periderm present on root and lower portions of stems, originating in the first subepidermal layer. Some phloem parenchyma cells are subdivided into strands of crystal-containing cells; the crystals are single and rhomboidal, or few per cell, but are not aggregated into druses as in cortical cells.

Leaf. Although linear, the leaf is slightly flattened as seen in transection (Fig. 13). Stomata are ranunculaceous and present on all portions of the leaf surface. A thick cuticle is present and is raised into an overarching hood external to stomata (Fig. 16). Chlorenchyma is two or three layers thick; cells are only a little longer than wide, are closely packed, and are not differentiated into palisade cells. Some chlorenchyma cells contain tannin, and an occasional druse-containing cell may be observed. Only a single main vein is present; a small veinlet may branch from this on either side. The main vein consists





FIGURES 7–12. Wood sections of *Empleuridium*. 7, 8. Stem, from *Goldblatt 3418* (MO).—7. Transection, cambium at left, pith at right.—8. Tangential section. A few elongate ray cells may be seen. 9–12. Root, from *Esterhuysen 34318* (RSA).—9. Transection, tracheids are thicker walled than in stem.—10. Tangential section. A single ray is present, upper left. 11, 12. Vessels from radial section.—11. Simple perforation plate (upper left); scalariform lateral wall pitting (right).—12. Perforation plate traversed by a single bar. Figures 7–10, scale above Figure 7 = 10 μm; Figures 11, 12, scale above Figure 11 = 10 μm.



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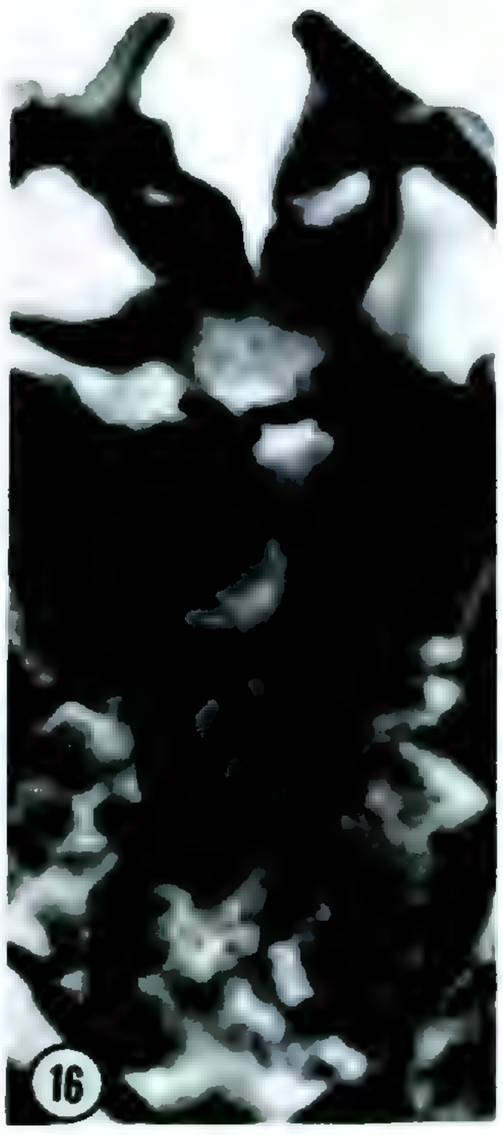

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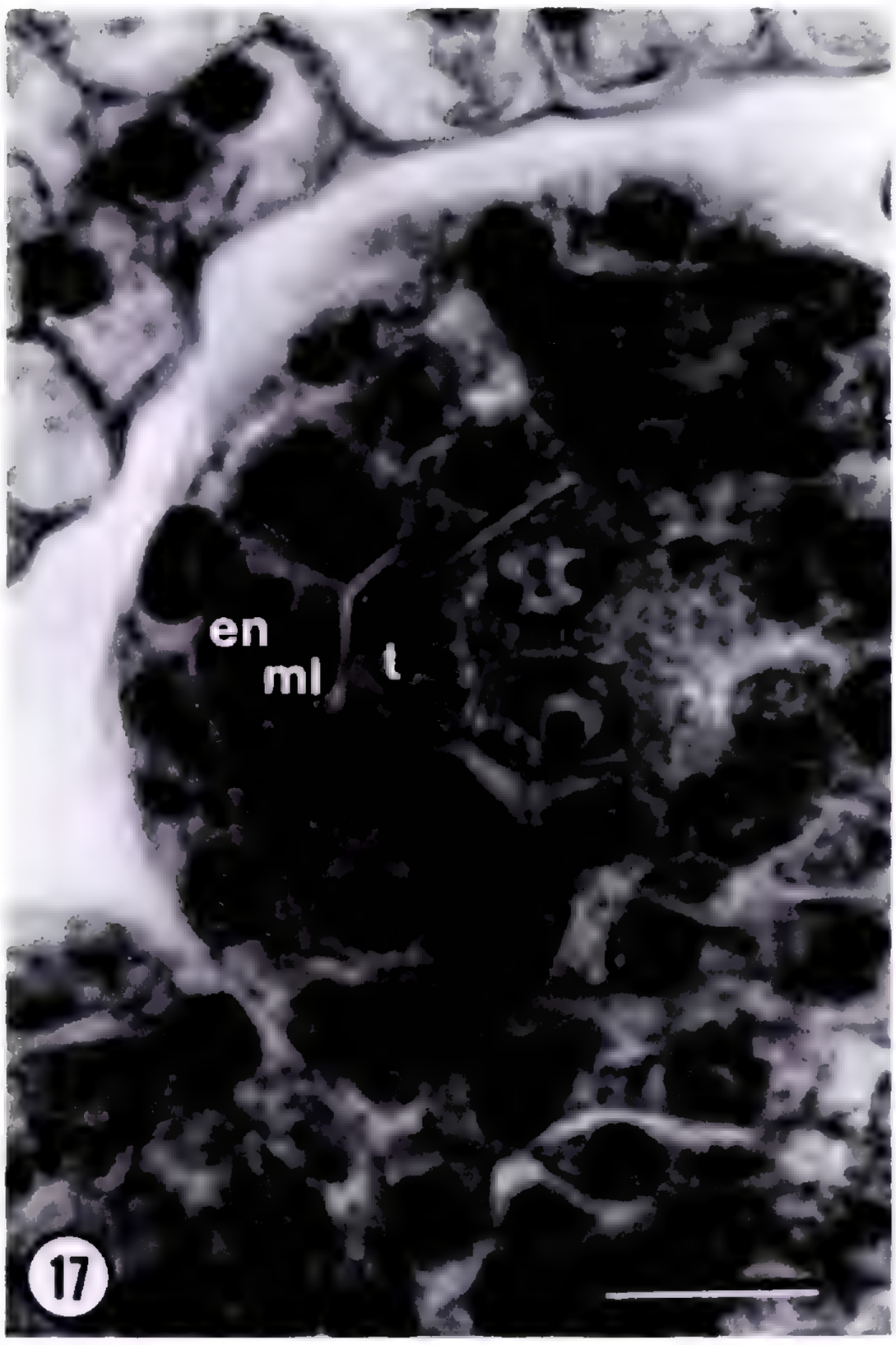
FIGURES 13–16. Sections of *Empleuridium*. 13, 14, 16, sections of leaf from *Goldblatt 3418* (MO).—13. Leaf transection, adaxial surface above.—14. Longitudinal section of vein in leaf; tracheids with scalariform and alternate circular pits at right, fiber at left.—15. Transection of cortex of root, from *Esterhuysen 34318* (RSA). Druses visible in some cells, tannin in others; periderm at right.—16. Stoma from leaf, showing overarching cuticular ridges. Figures 13, 15, scale above Figure 7; Figures 14, 16, scale above Figure 11.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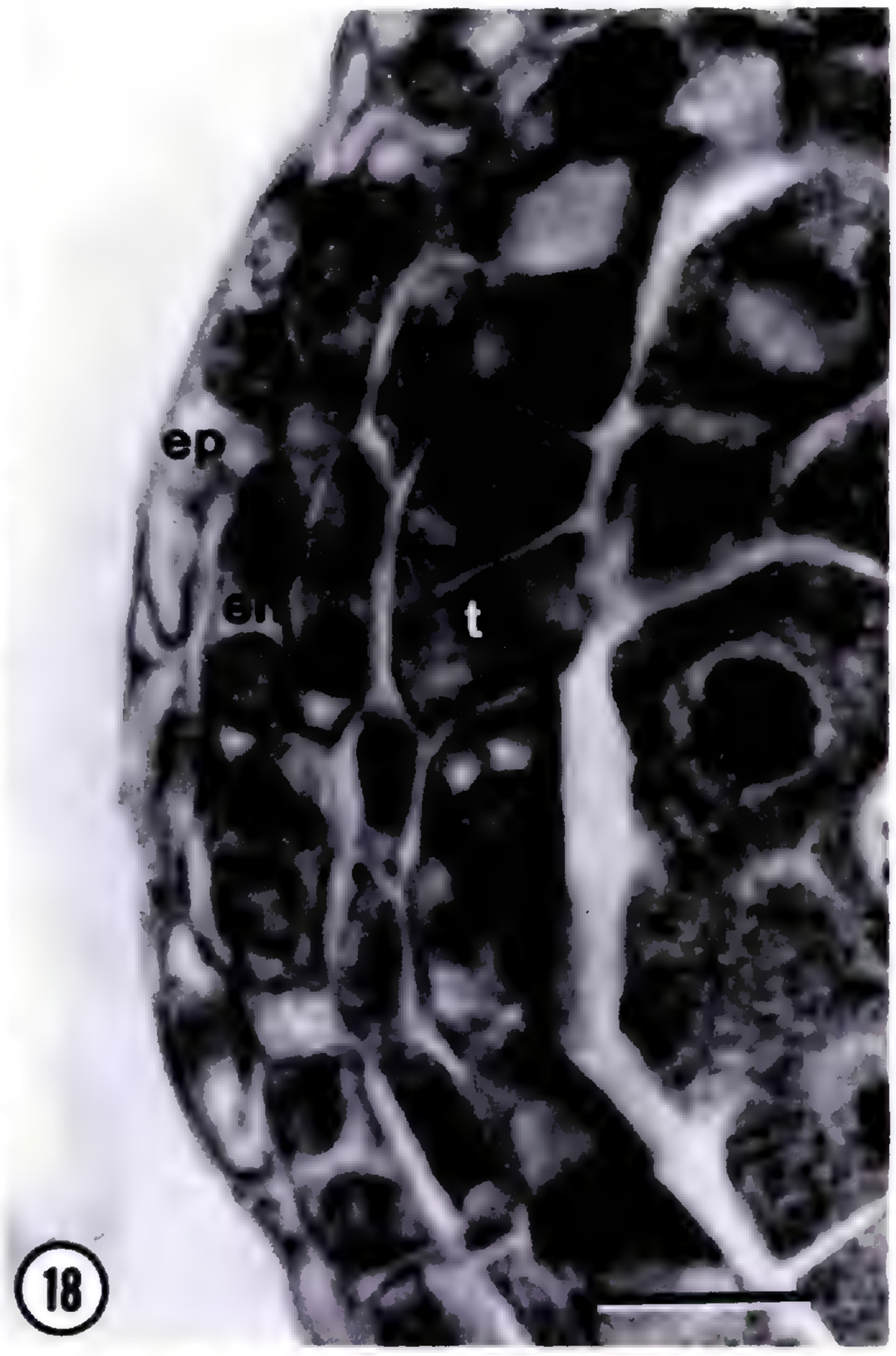
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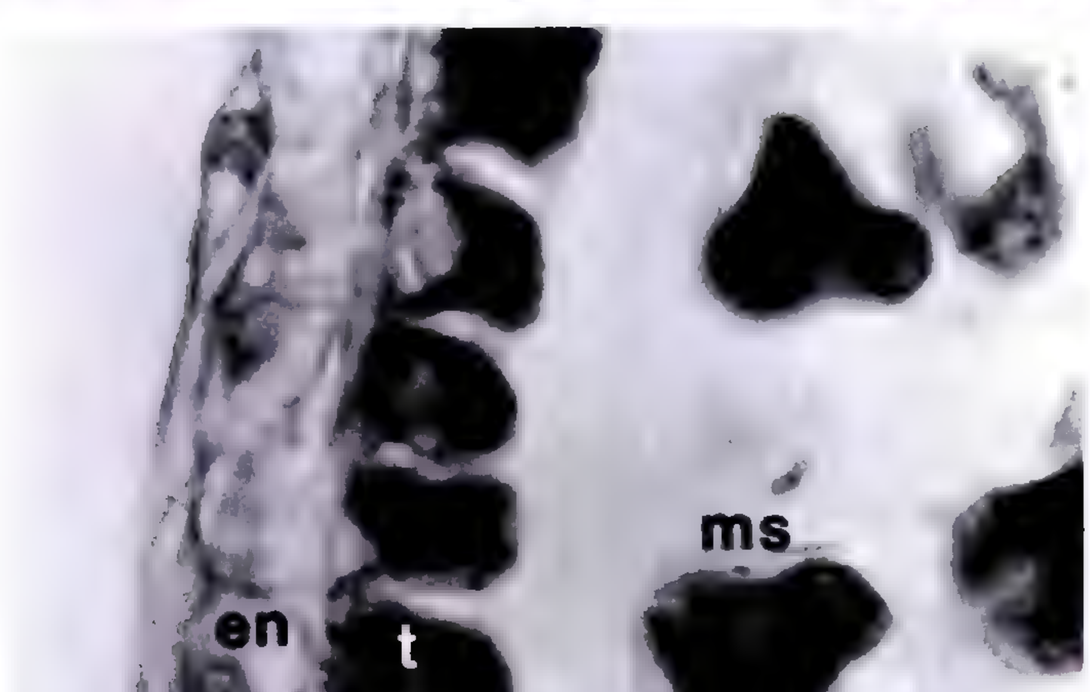
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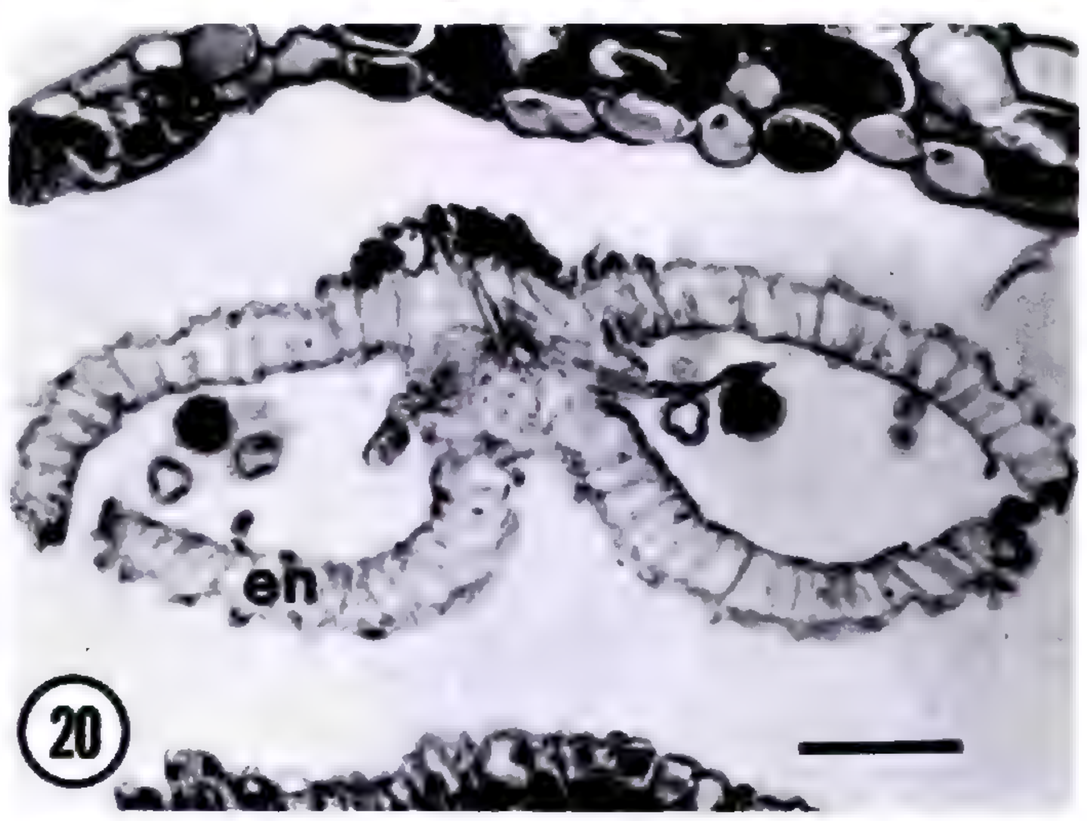
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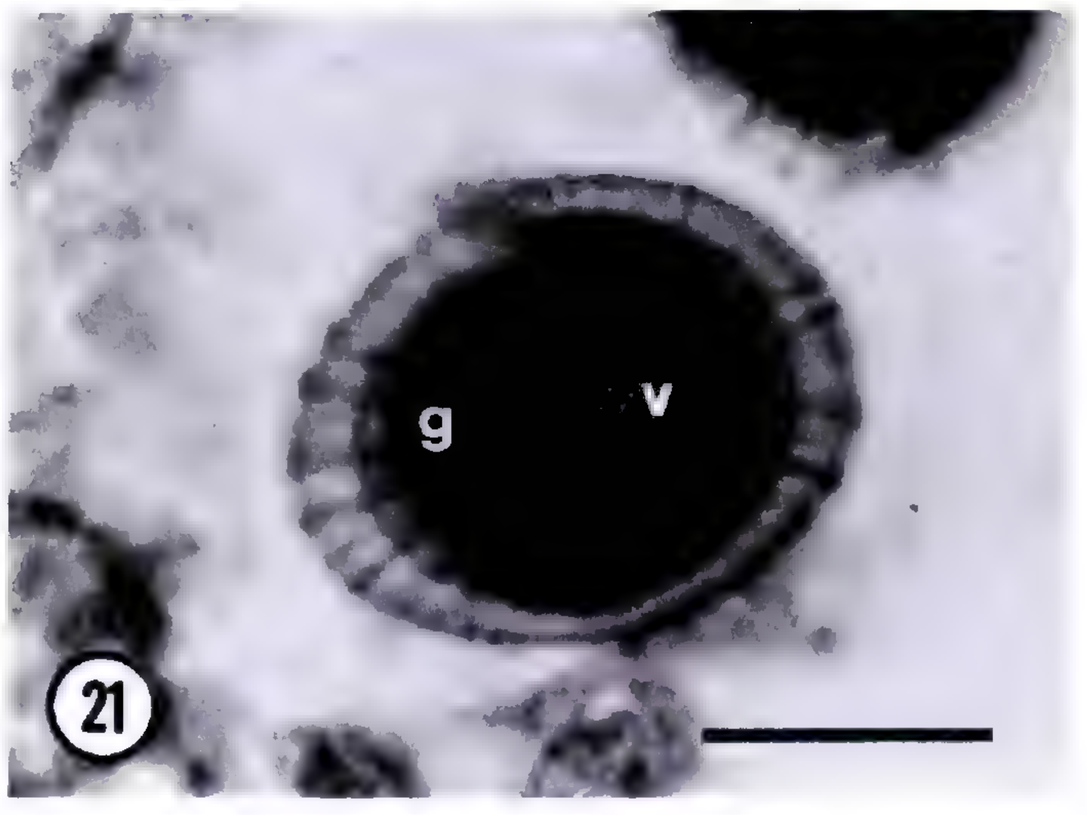
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of a laterally wide bundle sheathed adaxially and abaxially by fibers. The xylem of the vein consists of annular, helical, and scalariformly pitted tracheids, but also tracheids with circular bordered pits (Fig. 14, right). No secretory cavities were observed.

EMBRYOLOGY

Anther and microspores. The anther is tetrasporangiate. The wall structure prior to maturation comprises four layers; epidermis, endothecium, one middle layer, and tapetum (Fig. 18). Cells of the middle layer and endothecium are derived from the same cells (Fig. 17), and the wall formation is regarded as conforming to the dicotyledonous type (Davis, 1966). During maturation, the epidermis mostly collapses and the middle layer degenerates while the endothecium develops fibrous thickenings. The tapetum is glandular and its cells become two-nucleate (Fig. 19) and finally degenerate. Thus the mature anther wall at dehiscence consists principally of the fibrous endothecium (Fig. 20). Dehiscence is longitudinal.

Meiosis in microspore mother cells is accompanied by simultaneous cytokinesis (Fig. 19). The shape of the microspore tetrads, on the basis of the examination of 50 selected tetrads, is usually (94%) tetrahedral and very occasionally (6%) decussate (expressions for the frequency follow Schmid, 1982). Pollen grains are released singly and are two-celled (Fig. 21).

Megagametophyte and nucellus. The ovule is anatropous and tenuinucellate. A single archesporial cell differentiates beneath the apical dermal layer of the small nucellus (Fig. 22), and directly develops into a megaspore mother cell (Fig. 23). No case was observed in which two or more archesporial cells were borne in a single nucellus. The megaspore mother cell normally undergoes meiosis, resulting in a linear or T-shaped tetrad of megaspores (Fig. 24). The chalazal megaspore of the tetrad always functions and successively develops into a two- (Fig. 25), four- (Figs. 26, 27), and eight-nucleate *Polygonum*-type embryo sac. The synergids exhibit no particular specialization. Two polar nuclei are united into a central nucleus before fertilization (Fig. 28). The three antipodal cells are ephemeral and always absent in the organized mature embryo sac. Thus prior to fertilization, the embryo sac consists only of an egg, two synergids, and the central nucleus (Fig. 28).

During megasporogenesis and megagametogenesis, a remarkable breakdown of the nucellar tissue surrounding the megaspores or the embryo sac occurs (Fig. 24). As a result, the greater part of the embryo sac after the two- or four-nucleate stage is no longer enclosed by the nucellar tissue but borders directly on the inner integument (Figs. 25–28). The break-down of the remaining nucellar tissue continues until it almost disappears. In a young seed, the enlarged embryo sac is wholly surrounded by the inner integument alone. No hypostase is formed during the development of the ovule and seed.

Integuments and endothelium. The micropyle is formed by the inner integument alone (Fig. 29). Both the inner and the outer integuments are initiated by involving an oblique-periclinal or periclinal division of dermal cells in an ovule primordium (see arrows in Fig. 30). The subsequent growth of the integument takes place by the division of cells derived from the dermal initials, while the subdermal cells do not contribute to the formation of the integuments. The integuments are thus regarded as being of "dermal origin" (Bouman & Calis, 1977). As early as the megaspore mother cell stage both the integuments are usually three cell-layers thick. In older stages, the constituent cells further divide periclinally, so that the outer integument becomes four cell-layers thick while the inner integument increases the thickness into more than six cell-layers. Neither the outer nor the inner integument is vascularized. A vascular bundle in the funiculus ends at the chalaza and does not exhibit post-chalazal branching.

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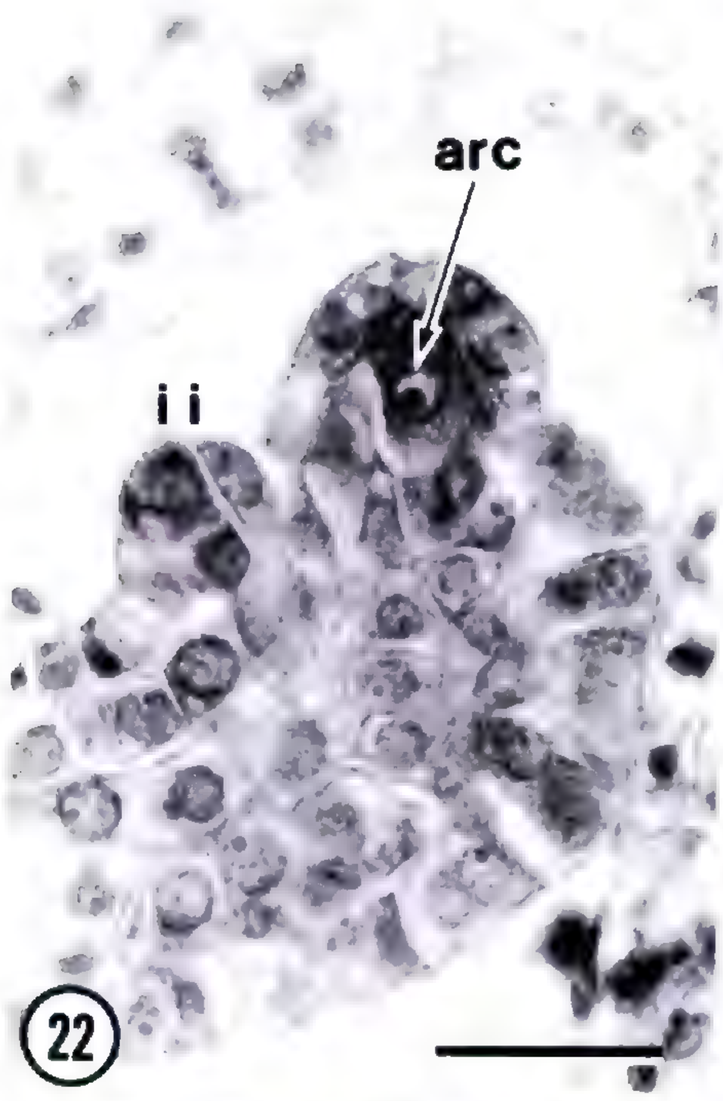
FIGURES 17–21. Development of anther walls and microspores in *Empleuridium*. ep, epidermis; en, endothecium; ml, middle layer; t, tapetum; mc, microspore mother cell; ms, microspores in telophase of meiosis II; v, nucleus of the vegetative cell; g, nucleus of the generative cell.—17. Transverse section (TS) of a young anther. Scale = 10 μm.—18. TS of an older anther than that shown in Figure 17. Scale = 10 μm.—19. TS of an older anther than that shown in Figure 18. Scale = 10 μm.—20. TS of a mature anther. Note that the wall comprises the fibrous andothecium alone. Scale = 100 μm.—21. Section of a mature pollen showing the two-celled state at the time of shedding. Scale = 10 μm.



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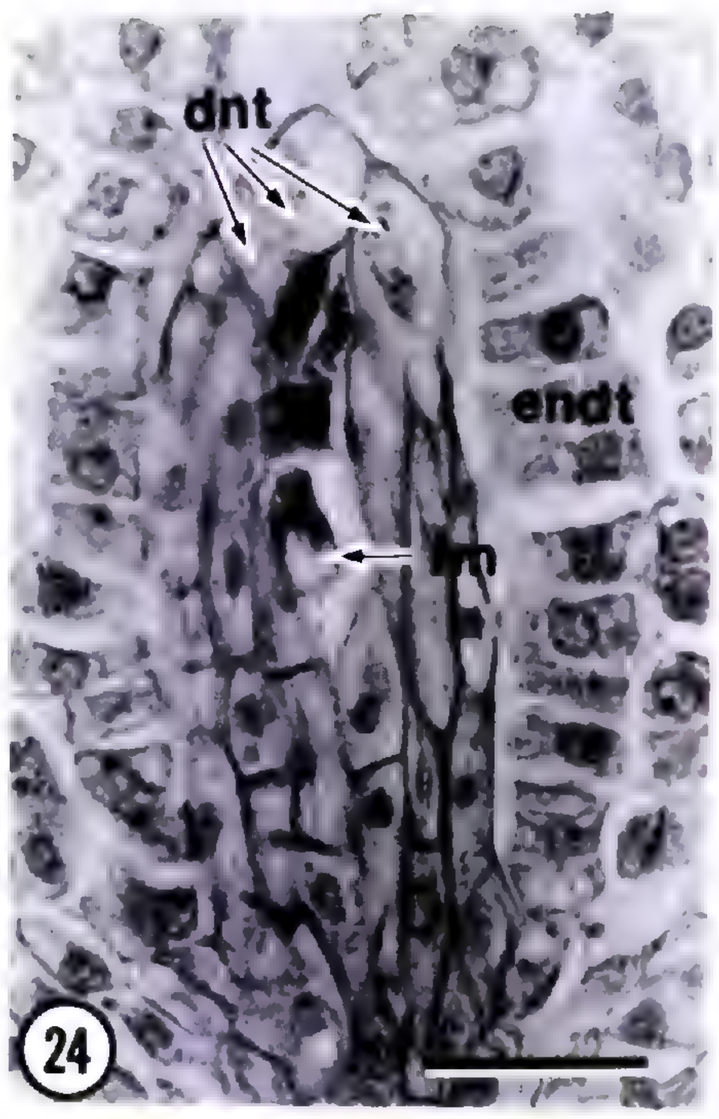

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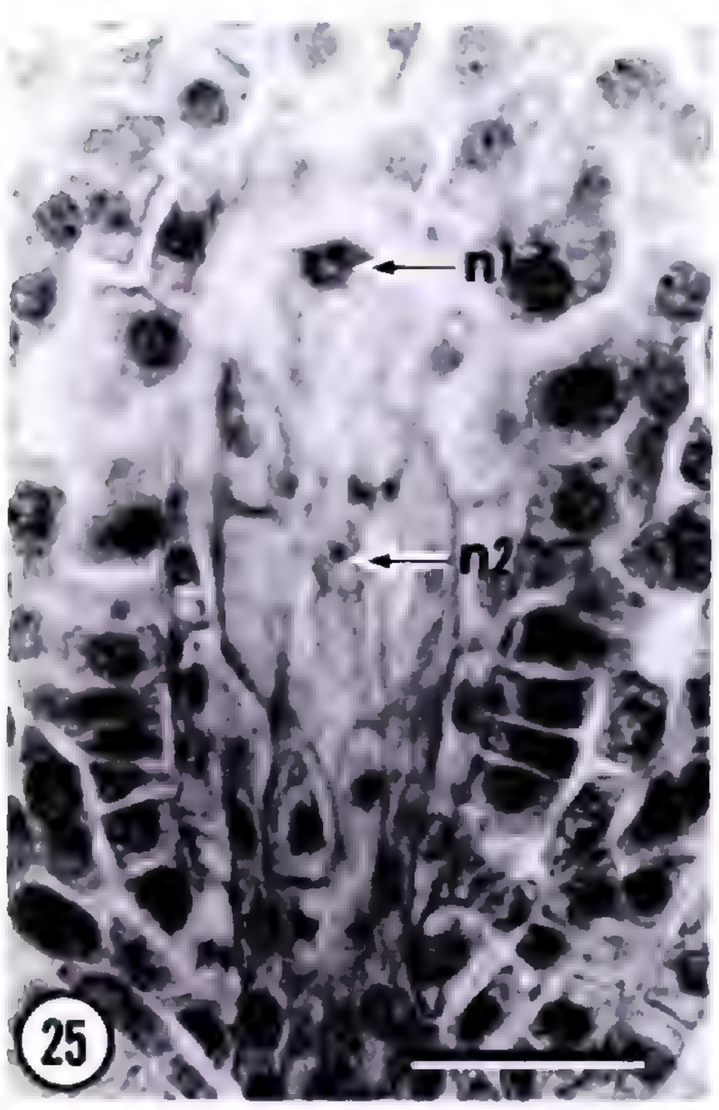

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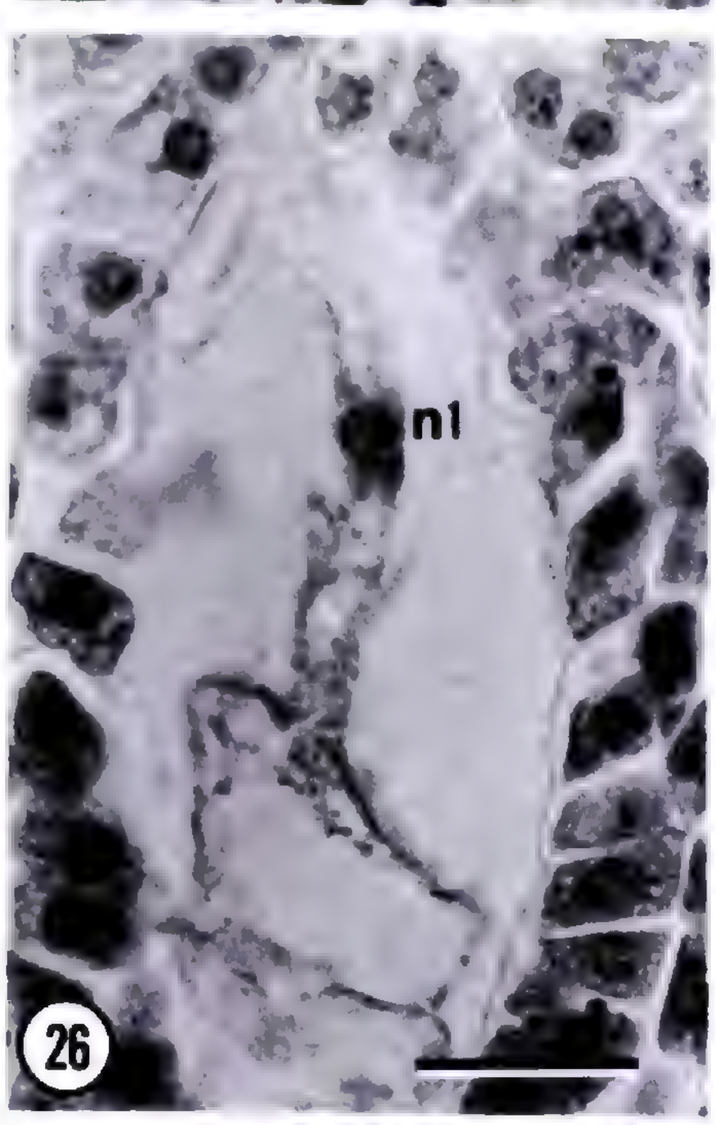

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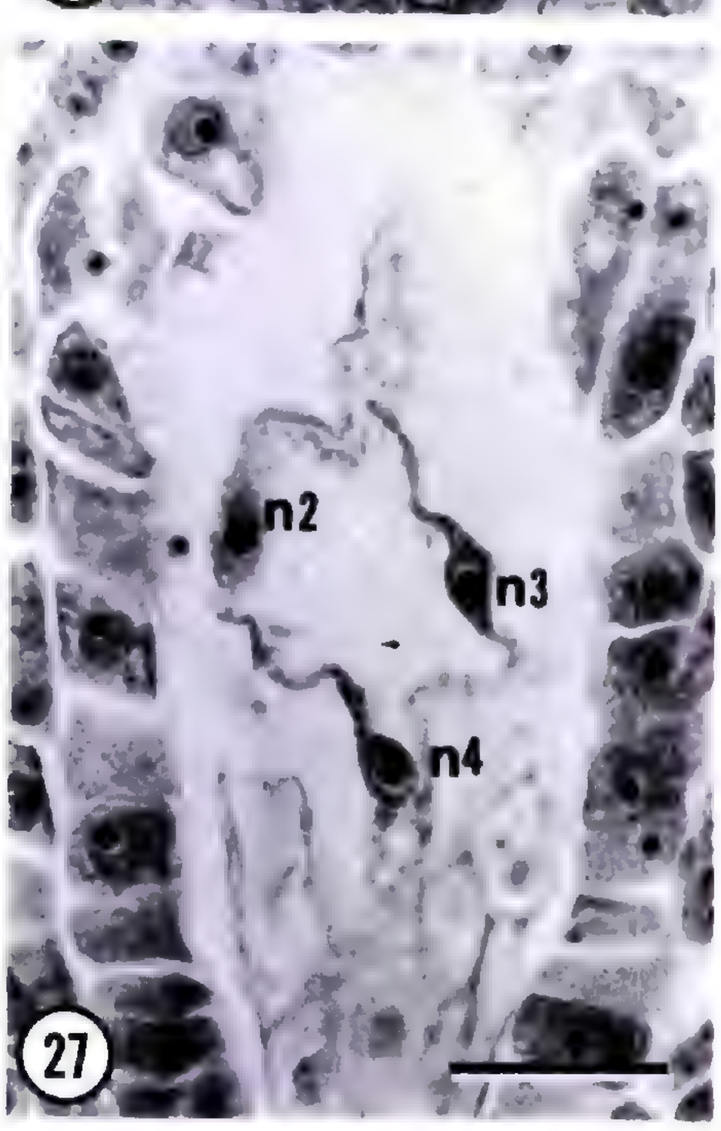

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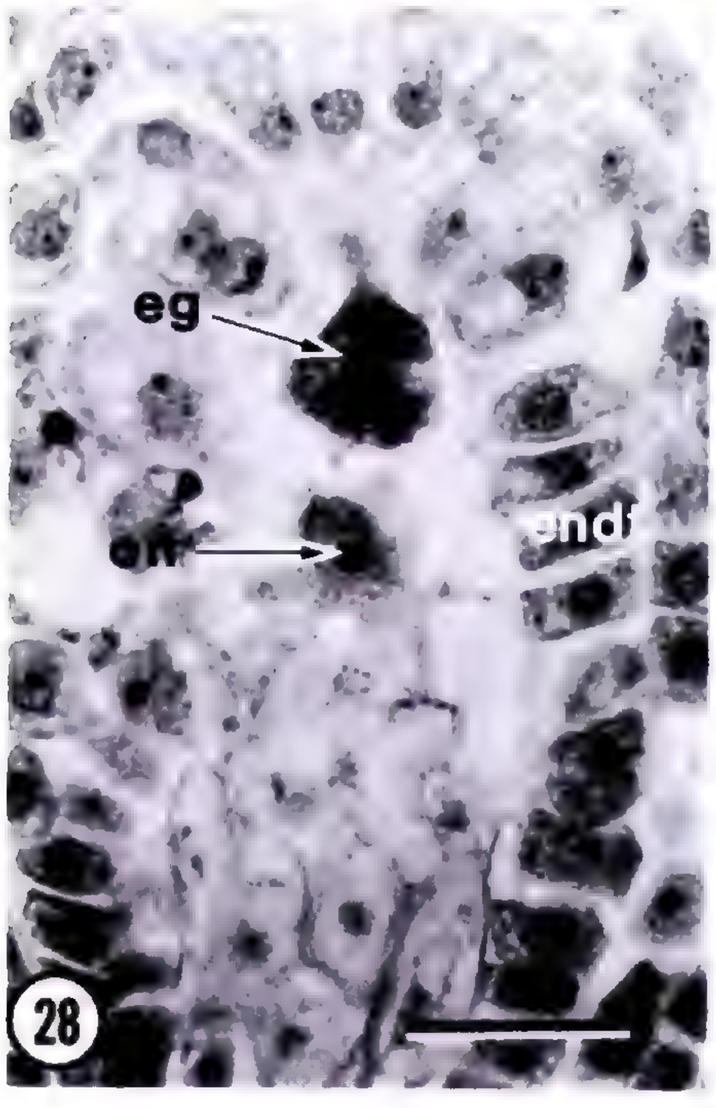

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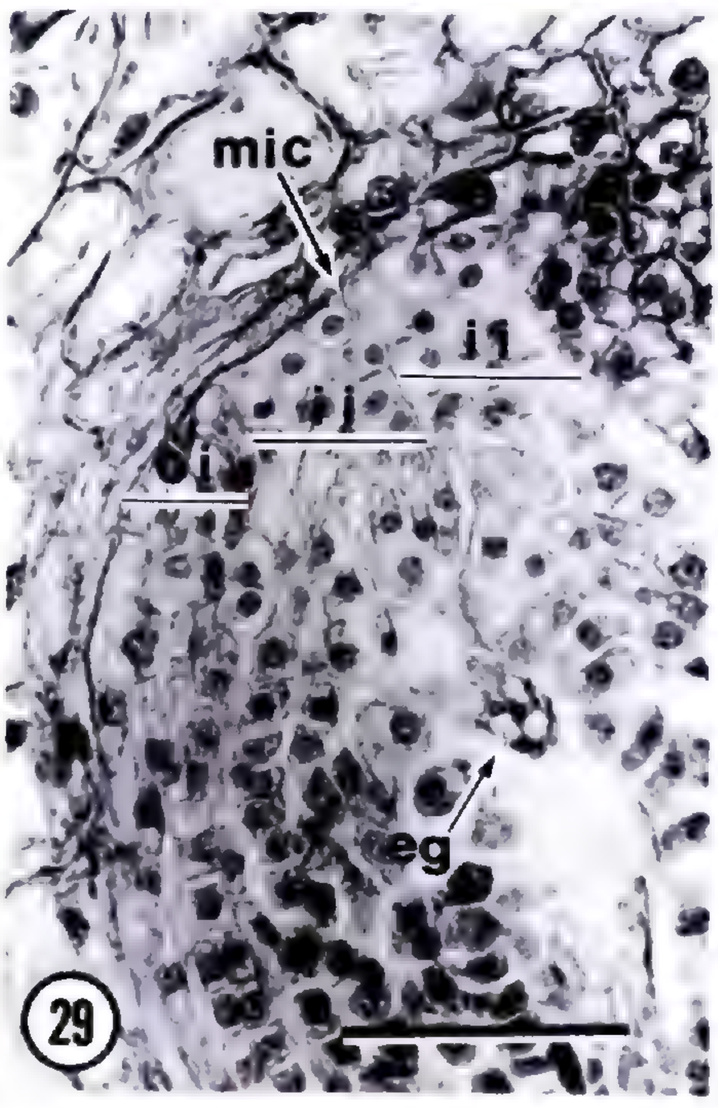

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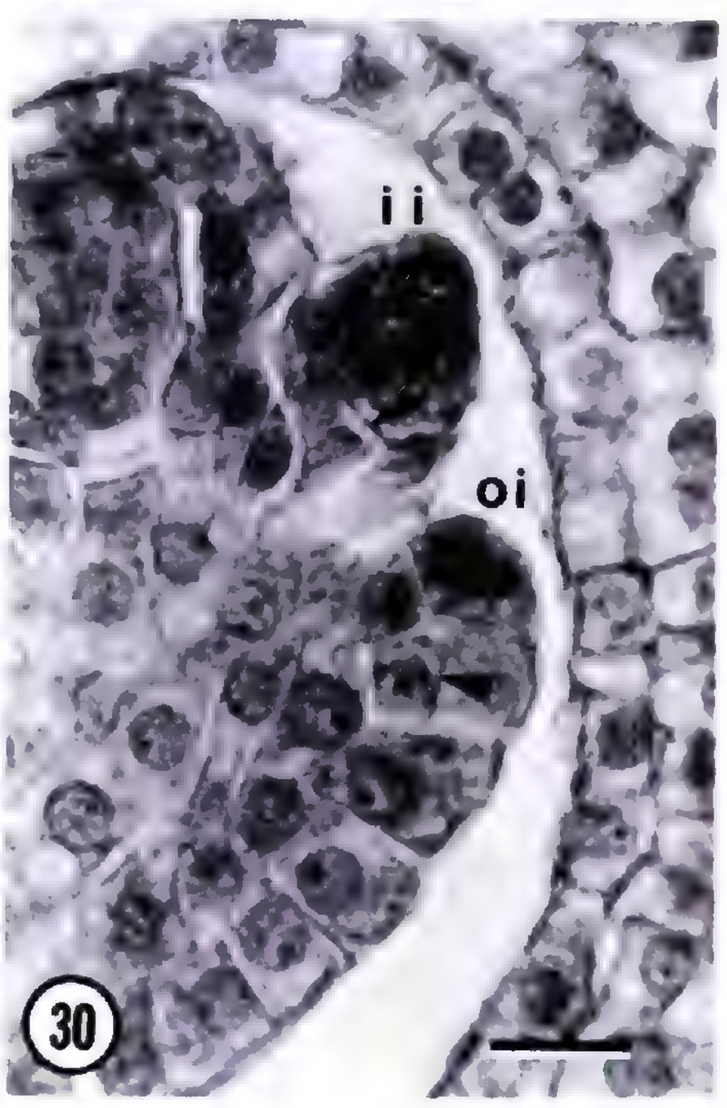

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As the nucellar tissue breaks down and the embryo sac comes to border directly on the inner integument, cells of the inner layer of the inner integument become somewhat radially elongated and enlarged (Figs. 24, 28) to form a weakly developed endothelium (i.e., integumentary tapetum).

Fertilization, endosperm, and embryo. Fertilization is porogamous and endosperm formation is nuclear. Wall formation in free endosperm nuclei occurs in later stages, and the young seed is filled with a cellular endosperm. The mature seed is albuminous with copious endosperm (Fig. 31). The endosperm is oily.

Our fruit samples were not adequate to pursue the embryogeny, but based on microtome sections of several proembryos, the embryogeny of *Empleuridium* appears to proceed normally. A suspensor appears to be small and short. The mature embryo is narrow, straight and dicotyledonous (Fig. 31). Both cotyledons develop equally. The mature seed has a large white aril (elaiosome) (Fig. 33) formed by cells derived from the outer integument and probably from the funiculus. It consists of a cushion-like base connected to the micropyle and is drawn distally into coiled filaments. The surface is covered with minute trichomes (Fig. 34).

The seed coat is formed principally by cells of the exotesta and the exotegmen (Figs. 31, 32) that were previously those of the outer layer of the outer and the inner integument, respectively. In the testa, only the cells of the exotesta are persistent and become tanniferous and cuboidal in shape while cells of the remaining part are completely crushed. The cells of the exotegmen are elongate longitudinally and radially, though the longitudinal elongation is more conspicuous, and become fibrous with pits at places; in addition, cells of the endotegmen that previously formed the endothelium, become slightly elongate longitudinally and tanniferous; cells of all the remaining parts are completely crushed.

POLLEN

The pollen grains are tricolporate, radially symmetric and isopolar, subprolate in lateral view (Figs. 35, 37), and triangular-pleurotreme in polar view (Fig. 36). The surface is reticulate with the widest lumina at the poles (Figs. 35–37). Lumina size decreases toward the equator (Fig. 35) with the smallest lumina around the colpi (Fig. 37). Columellae supporting the muri (i.e., the lumina ridges) are spindle-shaped, unbranched, erect, and with lengths directly proportional to lumina size. Colpi are wide and have a coarse surface. Endoapertures are large, lalongate, and elliptic with rounded ends. The polar axis is ca. 26 μm and the equatorial diameter is ca. 21 μm.

DISCUSSION

RELATIONSHIPS

Empleuridium does not belong in Rutaceae nor to any families in this alliance. It was assigned here when the nature of the gynoecium was unknown and the genus was believed to be dioecious. *Empleuridium* is discordant with Rutaceae in having a nonglandular floral disc; the five stamens alternate with the petals rather than opposite to them; an inferior, non-septate unilocular ovary probably composed of four fused carpels; a single-seeded fruit; and in entirely lacking glands in the leaves and other organs (Cronquist, 1981). At the embryological level *Em-*

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FIGURES 22–30. Development of ovules and megagametophytes in *Empleuridium*. arc, archesporium; mc, megaspore mother cell; fm, functional megaspore; n1 and n2, two nuclei in the two-nucleate embryo sac; n1–n4, four nuclei in the four-nucleate embryo sac; eg, egg apparatus comprising an egg cell and two synergids; cn, central nucleus formed by fusion of two polar nuclei; ii, inner integument; oi, outer integument; endt, endothelium; dnt, degenerating nucellar tissue; mic, micropyle.—22. Longitudinal section (LS) of an ovule primordium at the archesporial cell stage. The archesporium is one-celled. Scale = 20 μm.—23. LS of an ovule primordium at the megaspore mother cell stage showing the tenuinucellate condition. Scale = 20 μm.—24. LS of a young ovule at the megaspore tetrad stage. Note that the tissue of the upper part of the nucellus is degenerating. Scale = 20 μm.—25. LS of a young ovule at the two-nucleate embryo sac stage. Note that the embryo sac directly borders on the inner integument. Scale = 20 μm.—26, 27. Two successive LSs of a young ovule at the four-nucleate embryo sac stage. Scale = 20 μm.—28. LS of a mature ovule with an organized *Polygonum*-type embryo sac. Antipodal cells are not seen because of their ephemeral nature. Scale = 20 μm.—29. LS of a mature ovule showing the micropyle formed by the inner integument alone. Scale = 50 μm.—30. LS of an ovule primordium showing the mode of initiation of integuments. Arrowheads indicate that both the integuments are initiated by oblique-periclinal or periclinal divisions of dermal cells of the ovule primordium. Scale = 10 μm.

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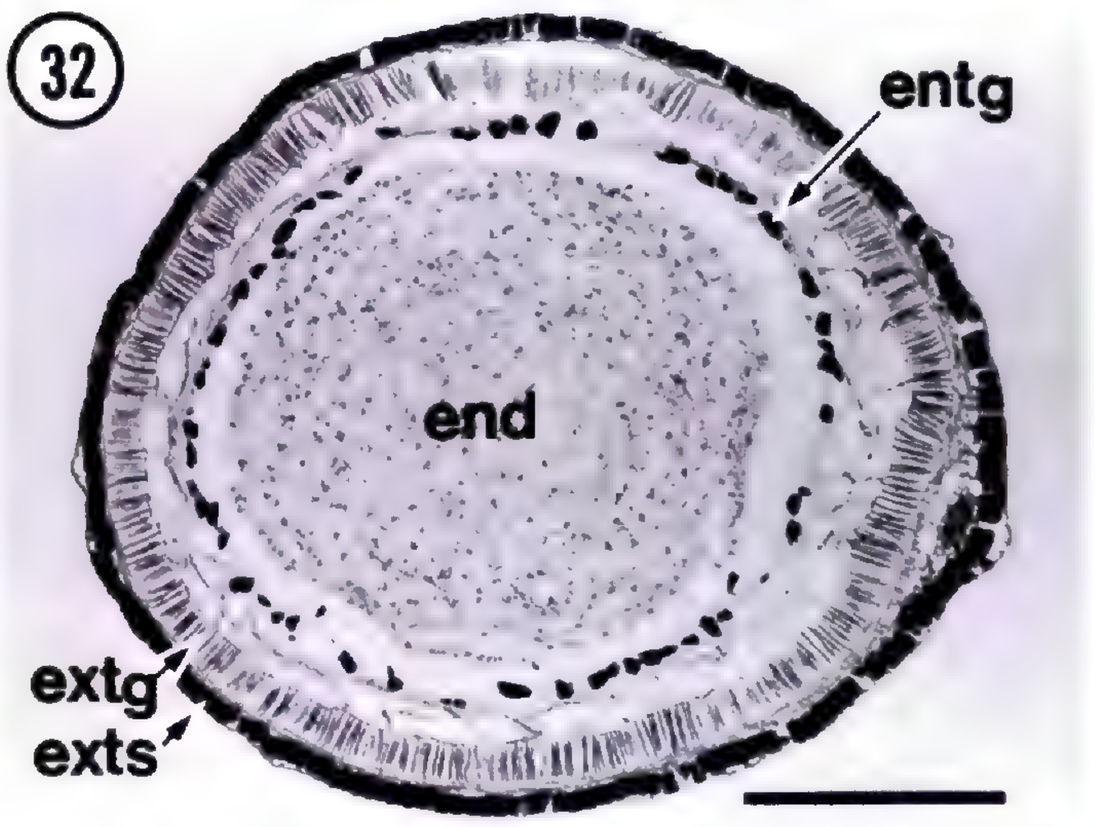
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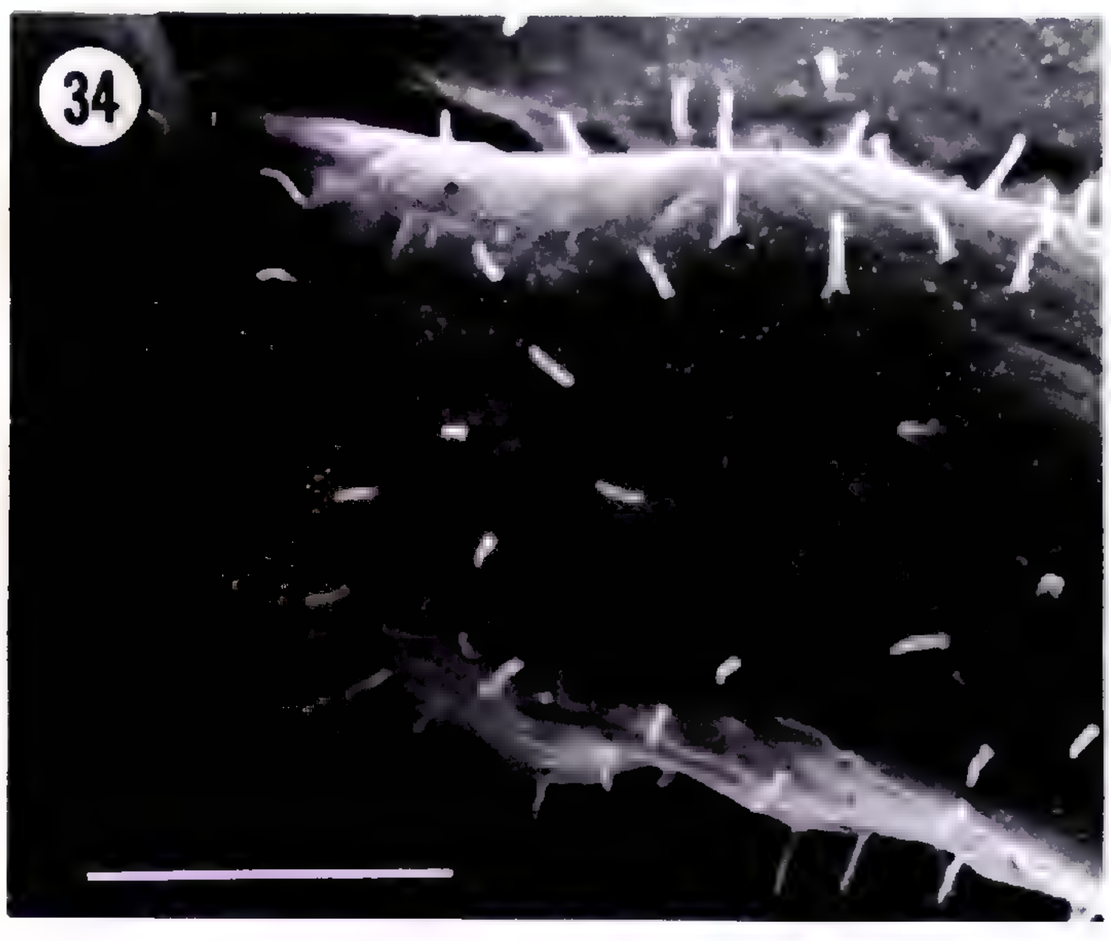
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pleuridium contrasts with Rutaceae in having two-nucleate anther tapetum cells in contrast to two multinucleate cells forming polyploid masses by fusion (Johri & Ahuja, 1957; Desai, 1962); a nucellus that degenerates early (persistent in Rutaceae); and the absence of a hypostase (Mauritzon, 1935, 1936; Davis, 1966). Vegetative anatomy also supports the exclusion of *Empleuridium* from Rutaceae. The wood has tracheids, rather than libriform fibers, and lacks the secretory cavities typical of Rutaceae (Metcalfe & Chalk, 1950).

Morphologically and embryologically, *Empleuridium* accords well with Celastrales in the broad sense (e.g., Cronquist, 1981), and once its characters are correctly interpreted it keys out to this order in standard keys to the flowering plants. It agrees with Celastraceae in particular, having small bisexual haplostemonous flowers, with a non-secretory floral disc, short filaments and a short persistent style. Embryological characters also accord with Celastraceae, notably the weakly developed and early degenerating nucellus, presence of an endothelium, and the arillate seed with oily endosperm (Berkeley, 1953; Copeland, 1966; Corner, 1976).

The anatomy of *Empleuridium* is relatively unspecialized. Most of its features are distributed widely in the dicotyledons (ranunculaceous stomata, druses, rhomboidal crystals, tannin cells). The relatively primitive wood with tracheids rather than libriform fibers suggests affinities with several orders with similar wood, e.g., Saxifragales, Rosales, as well as Celastrales. In fact, *Empleuridium* accords particularly well with Stackhousiaceae, an Australasian group related to Celastraceae, but morphologically very different from *Empleuridium* and clearly not directly related to it.

The strikingly reticulate surface, subprolate shape, tricolporate apertures, and size of *Empleuridium* pollen all agree with morphological descriptions of Celastraceae (Erdtman, 1971; Lobreau-Callen, 1977, 1978; Lobreau-Callen & Lugardon, 1972–1973). In personal correspondence with D. Lobreau-Callen, the pollen authority for the Celastrales, *Empleuridium* is favorably compared with several members of the Celastraceae (viz., *Pterocelastrus rostratus, Mystroxylon aethiopicum, Plenckia bahiensis,* South African species of *Maytenus,* and some species of *Cassine*). A difference with Celastraceae pollen is apparent in the poor development or absence of an endexine fold in the aperture, a character heretofore noted in all members of the family (Lobreau-Callen & Lugardon, 1972–1973). *Empleuridium* pollen is distinguished within the family (and order) by the reticulum lumina which are larger at the poles than at the equator (see Fig. 35).

Empleuridium is discordant with Celastraceae in its being a low ericoid shrublet, and in floral structure in the inferior unilocular ovary and the micropyle formed from the inner integument alone. It is also unusual in its one-seeded fruit, basal placentation with erect ovules, and the remarkable aril with coiled filamentous extensions. However, in a few Celastraceae the ovary is sometimes nearly inferior (e.g., *Paxistima*) although usually superior or semi-inferior (Berkeley, 1953); the fruit is occasionally one-seeded (e.g., *Bhesa, Plenckia, Zinowiewia, Microtropia*) although usually many-seeded (Corner, 1976); and the ovule is sometimes basal and erect (e.g., *Euonymus, Behsa, Paxistima*) (Berkeley, 1953; Corner, 1976). There is even a comparable seed in the Malaysian *Sarawakodendron,* in which the aril has branched filaments on the cushion-like base (see Corner, 1976, vol. 2: 81).

Thus, as regards the reproductive characteristics, the difference between *Empleuridium* and Celastraceae seems to be limited to the non-septate and unilocular ovary and the micropyle formed by the inner integument alone. Even in these features there are examples that reduce the isolation of *Empleuridium.* In *Celastrus orbiculatus* Lam. the septa do not fuse in the center of the ovary (Berkeley, 1953), a condition that can be regarded as transitional from (septate) plurilocular to (non-septate) unilocular. The di-

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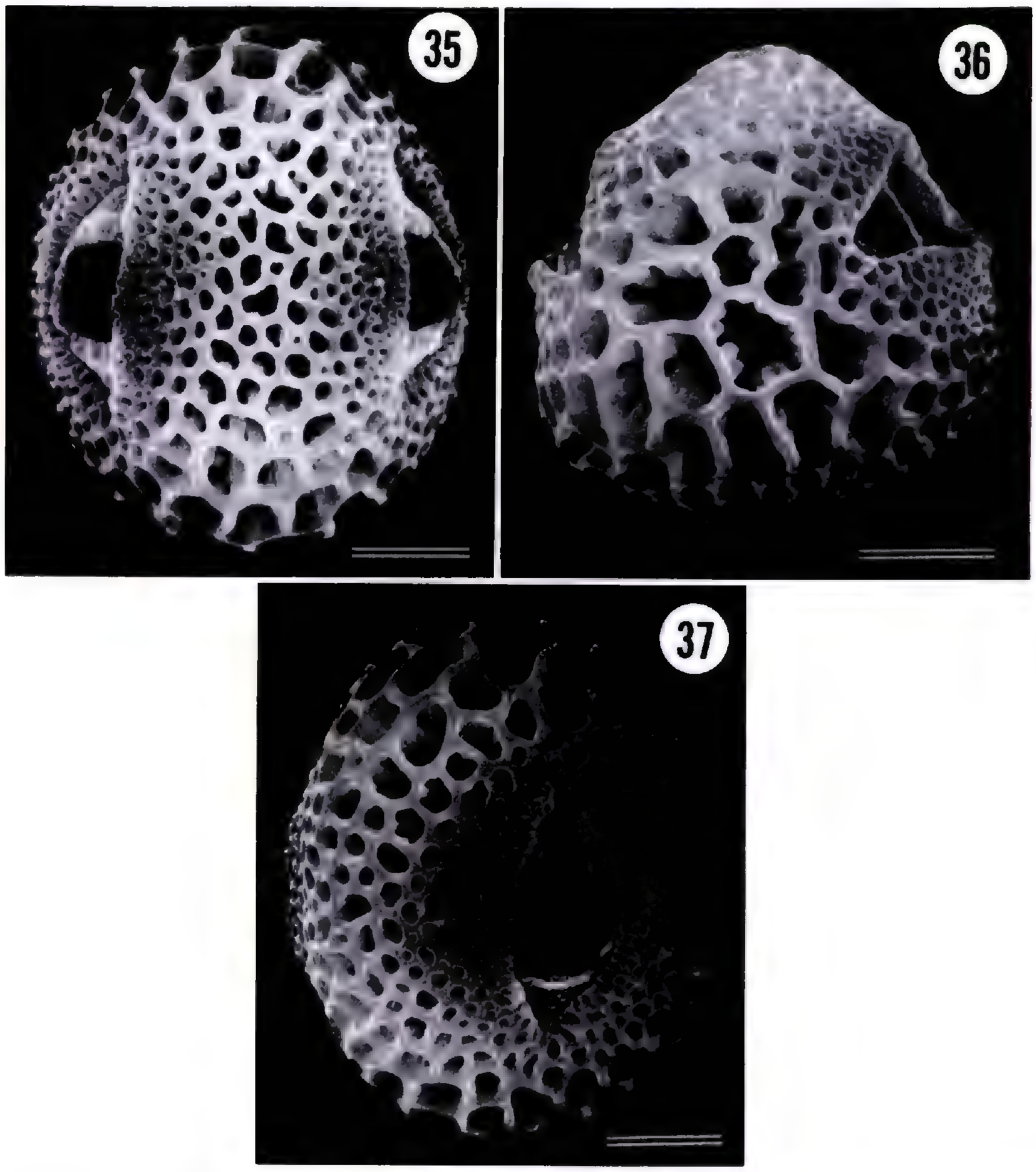
FIGURES 31–34. Seed and seed coat of *Empleuridium.* em, embryo; end, endosperm; entg, endotegmen; extg, exotegmen; exts, exotesta; ar, aril.—31. Longitudinal section of a micropylar half of the mature seed containing a straight embryo and the endosperm. Scale = 500 μm.—32. Transverse section of a nearly mature seed. Note the seed coat is formed principally by the exotesta and the fibrous exotesta. Scale = 200 μm.—33. Scanning electron micrograph of the mature seed showing an aril with elaborate structure. Scale = 1 mm.—34. Scanning electron micrograph of a part of the aril. Scale = 100 μm.



FIGURES 35–37. Pollen of *Empleuridium*.—35. Lateral view. The widest lumina are on the opposite poles with lumina at the equator. Scale = 5 μm.—36. Polar view emphasizing the wide lumina. Scale = 5 μm.—37. Lateral view. Around the margin of the colpus the lumina are greatly reduced. Scale = 5 μm.

versity of ovary structure in the Celastraceae is far from thoroughly studied, and similar trends for carpel fusion and septa reduction may occur in other members of the family, not necessarily closely related to *Empleuridium*. The micropyle of the Celastraceae, however, is formed by both the inner and the outer integuments in all representatives of the family so far examined (Adatia & Gavde, 1962). The number and the kind of the components of the micropyle is a very important taxonomic character at higher levels, but the significance of the condition in *Empleuridium* should perhaps not be emphasized.

ANATOMY

The very narrow vessels of *Empleuridium* stems, ca. 15 mm in diam., are noteworthy. Few

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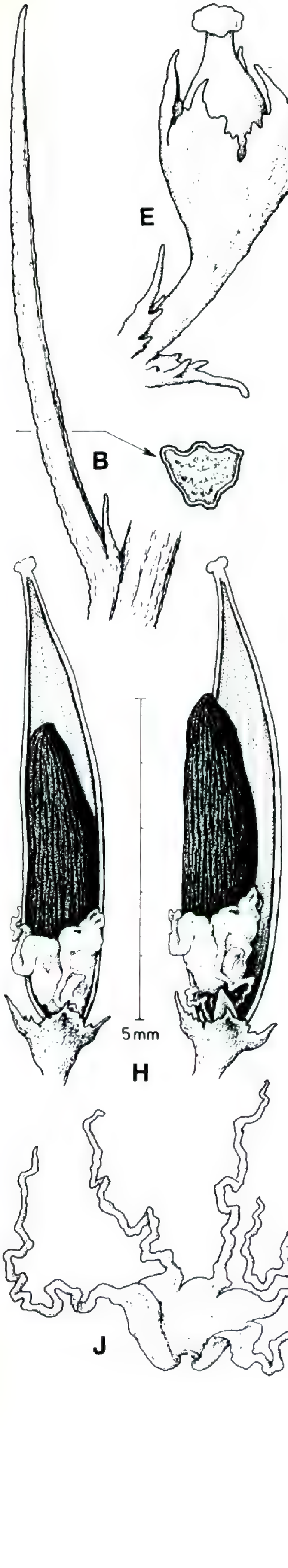
FIGURE 38. Morphology of *Empleuridium*.—A. Branch with ripe fruits as well as flowers.—B. Leaf with small subulate stipules.—C. Flower buds.—D. Flower after anthesis, the anthers shed.—E. Flower in even later stage.—F. Same, longitudinally sectioned.—G. Fruit in stage of dehiscence.—H. Fruit, half of the wall removed to show the single arillate seed; the aril is partly removed in the right figure, so that the conical funicle is exposed.—J. Aril, removed and laid open. All from *Esterhuysen 34318* (LD, C). Del. B. Johnsen (orig.).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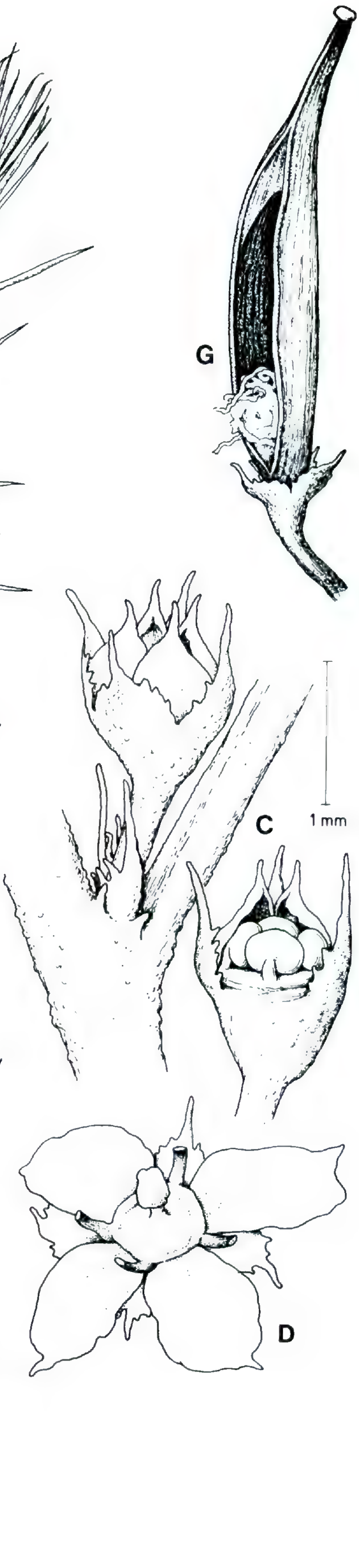
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dicotyledons characteristically have vessels this narrow, although Metcalfe and Chalk (1950) reported vessels of about 15 μm diam. in such species as *Bergenia delavayi* (Franchet) Engl. (Saxifragaceae). Vessel elements so narrow, so short, and so numerous per sq. mm of transection as those of *Empleuridium* are clear indicators of xeromorphy (Carlquist, 1977). The wood of the root of *Empleuridium* is somewhat less xeromorphic than that of the stem according to these measures. Wood of roots is generally more mesomorphic than that of stems (e.g., Carlquist, 1978; Carlquist et al., 1983).

The simple perforation plates in the xylem of *Empleuridium* are also an indicator of xeromorphy. Perforation plates with one to three bars, which are occasional in the species, seem relictual of a more primitive condition. They are sufficiently regular in appearance that they cannot be considered a malformation. The scalariform lateral wall pitting on vessels might be a remnant of a primitive condition, although a pseudoscalariform expression (lateral widening of pits based on an ancestry of alternate circular pits) cannot be ruled out.

The occurrence of tracheids in *Empleuridium* wood rather than fiber-tracheids or libriform fibers is a primitive feature in the wood, despite the specialization of perforation plates in vessels. The combination of simple perforation plates in vessels with occurrence of tracheids as the imperforate tracheary element type has been noted as unusually abundant in woods of dry areas, notably chaparral and desert (Carlquist, 1980; Carlquist et al., 1983). The adaptive value of this formulation is the ability to conduct water rapidly during the brief periods when it is available, permitted by simplification of the perforation plates, combined with the safety of tracheids (adapted for conduction, but air embolisms formed under water stress do not spread from one tracheid to another as they do with vessel elements).

The wood of *Empleuridium* is nearly rayless. In dicotyledons at large, raylessness characterizes herbaceous dicotyledons that are undergoing phylesis to woodier stature (Carlquist, 1970). *Empleuridium* is not very woody: it can be described as a diminutive woody herb. The raylessness (or presence of uniseriate rays, composed of erect cells only) in *Empleuridium* can be considered related to its habit. There is so little wood accumulation that one cannot say that this genus is in the process of becoming woodier.

The leaf of *Empleuridium* shows several adaptations to xeromorphy, such as condensed form, thick cuticle, cuticular domes over stomata, and isolaterally distributed chlorenchyma with rather small intercellular air spaces. The presence of unilacunar nodes in *Empleuridium* may also be related to the condensed linear leaves, because many species with linear leaves have unilacunar nodes, even in groups in which broader-leaved species have trilacunar nodes.

SUMMARY

It seems reasonable to assume that *Empleuridium* is a highly specialized member of Celastraceae, and that the unusual features of its flower and fruit are reductions from the basic type for Celastraceae. Clearly its small size, reduced woodiness, and needle-like leaves are specializations comparable with many other examples found in the Cape Flora, where a shrubby microphyllous habit is found in numerous taxa that in many cases have broad-leafed relatives. The specializations in wood anatomy reflect the adaptation to a Mediterranean climate by a small ericoid subshrub, based on a plan compatible with celastraceous woods.

SYSTEMATIC TREATMENT

Empleuridium Sonder in Harvey, Thesaurus Capensis 1: 49. 1859; Flora Capensis 1: 442. 1860; Phillips, Genera S. African Fl. Plants, ed. 1. 353. 1926; ed. 2. 442. 1951; Dyer, Genera Southern African Fl. Plants 1: 292. 1975. TYPE: *E. juniperinum* Sonder & Harvey. Figure 38.

E. juniperinum Sonder & Harvey, Thesaurus Capensis 1: 49–50. 1859; Flora Capensis 1: 442. 1860. TYPE: South Africa. Cape Province: "Bergrucken zwischen Caledon und Babylonschetoorn, 1,000–2,000 ft.," *Ecklon & Zeyher s.n.* (52.8) (S).

Ericoid, erect, glabrous, eglandular, undershrub. Leaves simple, needle-like, scattered, 9–11 mm long, with small scale-like stipules. Flowers axillary, solitary, small, tetramerous, actinomorphic, with a non-secretory receptacular disc, aestivation imbricate; pedicels 1.5–2 mm long, elongating to 3 mm in fruit, with small, paired opposed, scale-like bracts at the base; sepals 4, persistent, ovate, acute; petals alternate to the sepals, whitish, ovate, acute, free, spreading. Stamens 4, opposite the sepals, erect, fila-

ments short, ca. 1 mm long, anthers with 2 thecae, introrse. Ovary hemi-inferior, initially embedded in the receptacular disc, elongating well beyond the level of petal and stamen insertion after anthesis, unilocular, with 4 erect, basal ovules; style short, persistent, stigma capitate. Fruit large, ca. 7 mm long, fusiform, follicle-like, 1-seeded, dehiscing entirely along one suture; seed black, large, ca. 3 mm long, with a large white basal aril (elaiosome).

Distribution. SW Cape, mountains in the Caledon district, mainly above 600 m, on rocky sandstone slopes.

Material examined. 33.19 (Worcester) Blokkop (Aasvogelberg) above Villiersdorp, sun and shade at the rocky summit, ca. 5,200 ft. (CD), *Esterhuysen 35233* (BOL, NBG, S), *35575* (BOL, S).

34.19 (Caledon) Groenland Mts., Mt. Lebanon, 3,600–3,800 ft. (AA), *Goldblatt 6918* (MO); Mt. Lebanon above De Rust, ca. 3,000 ft., local, *Esterhuysen 34318* (BOL, NBG, MO, S); "bergrücken zwischen Caledon und Babylonschetoorn, 1,000–2,000 ft." (?AC), *Ecklon & Zeyher s.n.* (52.8) (S).

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WHY DO SOME COMPOSITAE HAVE AN INCONSISTENTLY DECIDUOUS PAPPUS?[1]

A. SHMIDA[2]

Many species of Compositae produce seeds equipped with a pappus that acts as a parachute, allowing the seeds to be dispersed by wind (Zohary, 1937, 1950; Pijl, 1972; Burtt, 1961, 1977). Surprisingly, in some other species the pappus is formed but deciduous, i.e., separates very easily from the body of the seeds, usually before dispersal. This trait seems paradoxical—why manufacture a dispersal apparatus and then drop it before dispersal? To our knowledge, no adaptive value for deciduousness has been put forward in the literature. Nonetheless, deciduousness is a common phenomenon recorded in Compositae from virtually all tribes, regions, and habitats.

As an initial stage in investigating possible adaptive values of a deciduous pappus, I have analyzed the Compositae in the flora of Israel for correlations between deciduousness and other ecological parameters. The results of this survey, which I present here, suggest that inconsistent deciduousness is adaptive primarily as a mechanism for achieving a mixed dispersal strategy, in which seeds that lose their pappus prior to dispersal remain in the vicinity of the mother plant ("atelechory" sensu Ellner & Shmida, 1981).

The analysis is based on Feinbrun-Dothan (1978) supplemented by extensive observations of species distributions and seed characters in Israel. Several species which have been found only sporadically in Israel, and appear not to be established in the flora, were excluded from the analysis. Seeds bearing only a few pales or awns, or a corolla, were regarded as epappose. Copies of the species-list with scorings for all attributes used in the analysis are available on request.

Associations between deciduousness and other attributes were examined by constructing 2 × 2 contingency tables in which the rows were defined by deciduousness versus persistence of the pappus, and the columns by presence versus absence of the other attribute. The tables were tested for significance at the level $\alpha = 0.05$ by either the chi-square test or (if any of the expected cell counts were ≤ 5) the exact multinormal test for a 2 × 2 table.

Of the 230 Compositae found in Israel, 42 have a deciduous pappus (DP), 112 have a persistent pappus, and the remainder are epappose. About half (22) of the species with a deciduous pappus are annuals. However, no significant associations were found between DP and growth-form (annual, biennial, perennial) or life-form (annual, hemicriptophyte, chamaephyte) in the Mediterranean region, the desert region, or both regions combined. I also investigated possible associations between DP and the following special habitats: Mediterranean region, desert region, rock outcrops, hygrophile and ruderal. A significant positive association was found between DP and ruderal habitats (Table 1a) (because all but two ruderals were classed as Mediterranean, only Mediterranean species were considered). However, this association appears to be an artificial consequence of two other associations: a strong negative association between DP and pappus dimorphism (Table 2), and a negative association between pappus dimorphism and ruderal habitats (Table 1b). If I remove this confusing trend by excluding species with a pappus dimorphism, there remains a positive but highly non-significant association between DP and ruderal habitats (Table 1c).

Thus, the only significant trend is that DP generally does not occur in species with pappus dimorphism. The term dimorphic pappus is used here in any case in which the achene of the same capitulum has more than one morphological type of pappus. The transition between type of pappus in the capitulum can be abrupt or gradual. The present article does not analyze heteromorphic achene, a phenomena which is correlated with heteromorphic pappus (Ellner & Shmida, 1981; Shmida & Ellner, in prep.). In the Compositae of Israel, pappus dimorphisms almost invariably involve a substantial reduction or complete elimination of the pappus on a portion of the achenes

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TABLE 1. Deciduous pappus and pappus dimorphism in relation to ruderal habitats in the Mediterranean region Compositae of Israel (cell entries are numbers of species).

	Ruderal	Non-ruderal
(a) Deciduous pappus[a]	16	15
Persistent pappus	20	52
(b) Pappus dimorphism present[a]	3	27
Pappus dimorphism absent	23	40
(c) Species without pappus dimorphism[a]		
Deciduous pappus	16	14
Persistent pappus	17	26

[a] The 2 × 2 tables in (a) and (b) (involving all Mediterranean region Compositae) depart significantly from independence ($\chi^2 = 4.42$ and 5.84, $P < 0.05$ and $P < 0.025$ respectively). The table in (c) (Mediterranean Compositae without a pappus dimorphism) does not depart significantly from independence ($\chi^2 = 0.86$, $P > 0.25$).

TABLE 2. Deciduous pappus in relation to pappus dimorphism in the Compositae of Israel (cell entries are numbers of species).

	Mediterranean Region[a]	Desert Region[a]	Entire Flora
Pappus dimorphism present[b]			
Deciduous pappus	2	2	4
Persistent pappus	14	24	38
Pappus dimorphism absent			
Deciduous pappus	14	25	38
Persistent pappus	32	46	74

[a] Five species found in both Mediterranean and desert regions are recorded in each.

[b] The paucity of dispersal-heterocarpic species with deciduous pappus is significant at $\alpha = 0.05$ in each region and in the entire flora (exact test for a 2 × 2 table applied to each column individually).

in each capitulum. DP and pappus dimorphism can therefore be viewed as alternative mechanisms which reduce the efficacy of wind-dispersal in some (but not all) seeds. The finding is that species tend not to utilize both alternatives. This is illustrated nicely in the genus *Crepis*: of the 12 species found in Israel, six have a deciduous monomorphic pappus, and six have a persistent pappus with a marked pappus dimorphism between marginal and central seeds in a capitulum (Feinbrun-Dothan, 1978). Similarly, in the *Filago* group (sensu Wagenitz, 1969; Feinbrun-Dothan, 1970), *Cymbolaena* and *Lasiopogon* spp. in Israel have a deciduous, monomorphic pappus, while in *Filago* and *Ifloga,* the central fertile achene in each capitulum has a persistent pappus and the marginal seeds are epappose (Feinbrun-Dothan, 1978).

These results suggest that DP and pappus dimorphism are alternative means to some end, but give no clue as to what that end might be. The most obvious conjecture has to do with seed dispersal distance. A pappus classed as "deciduous" may separate from the seed either before or after dispersal. My observations of *Lactuca* spp., *Carduus* spp., *Onopordon* spp., *Silybum marianum, Urospermum picroidis,* and *Notobasis syraica* indicate that some of the seeds produced by an individual lose their pappus before dispersal, while others lose their pappus only upon impact after dispersal.

DP and pappus dimorphism thus both result in a partial loss of "long-distance" dispersal by wind. Mixed dispersal strategies, in which some seeds disperse while others remain near the parent plant, have been found to be optimal in various models of species in spatiotemporally variable environments (Hamilton & May, 1977; Comins et al., 1980; Motro, 1982a, 1982b; Levin et al., 1983) and also in spatially structured but temporally constant environments (Hamilton & May, 1977; Motro, 1982a, 1982b). In patchy, variable habitats, dispersal allows a species to colonize suitable patches. Exploitation of suitable patches by subsequent generation requires retention of some seeds in the patch. Partial dispersal achieves both these ends, and a partial dispersal strategy is therefore generally optimal (Shmida & Ellner, 1984).

Other adaptive values for the lack of a pappus can also be conjectured. For example, epappose seeds may enter more readily into small cracks or openings in the soil, and buried seeds may avoid predation and thermal extremes faced by seeds lying at the soil surface (Ellner & Shmida, 1981). Conversely, epappose seeds are smaller and presumably easier for insect predators to handle.

The question remains, why produce a pappus if it is advantageous to lose it? Why not reduce or eliminate the pappus on some seeds? I hypothesize that the reason is evolutionary flexibility. A pappus "lost" by deciduousness can be regained by strengthening the attachment of pap-

pus to seed, a minor modification compared to redeveloping the entire pappus. However, the contemporary suggestion that a deciduous pappus can easily be reconverted to a functional condition (= high evolutionary flexibility) should be demonstrated experimentally in the future. The fraction of wind-dispersed seeds can therefore vary over ecological time. This feature would be most valuable in patchy, variable habitats where newly-created patches remain suitable for extensive periods, during which time non-dispersal would be favored, a hypothesis which should be tested in the future. When a patch starts to become unsuitable, dispersal would be favored.

Preliminary observations in the field with the Israeli Compositae flora indicate much variation within the dispersal dynamic of species with an inconsistently deciduous pappus:

a) The pappus can break before or after dispersal and the percentage of pre-dispersal breakage versus post-dispersal breakage changes within a capitulum, within a population.

b) Within the obligatory deciduous species known from the systematic literature, at least in some species, there is prominent variation in the field in the percentage of the capitulum's achenes which dispersed with or without a pappus. We hypothesize that such variation can serve has a dynamic mechanism of evolutionary flexibility toward selection (and reversed selection) of an adaptive phenomenon of a deciduous pappus on the whole, as well as the adaptability of an inconsistently deciduous pappus.

The large, spiny ruderals with deciduous pappi found on anthropogenic mounds of nitrogen-rich soil (species of *Carduus, Silybum, Notobasis, Cynara,* and *Onopordon*) may be an example of this syndrome. New mounds are constantly being created, and persist for several years. Populations of *Silybum marianum* and *Onopordon cynarocephalum* in different localities vary markedly in the fraction of seeds losing the pappus prior to dispersal (70–100% in ten populations of *Silybum,* 60–100% in three populations of *Onopordon*), possibly representing different phases in the cyclic selection for dispersal and non-dispersal, a hypothesis that should be tested.

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FINE STRUCTURE OF MISTLETOE POLLEN VI. SMALL-FLOWERED NEOTROPICAL LORANTHACEAE[1]

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ABSTRACT

Pollen of small-flowered neotropical Loranthaceae (8 genera; ca. 135 species) was examined in the light, scanning, and transmission electron microscopes. Pollen is typically medium-sized and oblate. Pollen *amb* is more variable than equatorial shape, ranging from trilobate deeply concave to circular. Both isopolar and heteropolar pollen grains occur within the complex, the latter restricted to species of *Phthirusa* and *Struthanthus* in which the apertures differ at each of the polar faces. Simple apertures arranged in a diploaperturate configuration predominate. Such apertures range from diploporate to diplobrevidemicolpate to diplosyn- and diploparasyndemicolpate types. Compound apertures are rare, restricted to *Oryctanthus* and particular species of *Cladocolea* and *Struthanthus*. The (3–)4–5 colpate apertures of *Ixocactus* are unique in the family. Sculpturing is basically uniform with sculpturing elements ranging from perforations to shallow ridges and/or striato-rugulae. Ultrastructurally, the basic ektexine structure is composed of a thin, perforate tectum, granular/columellate interstitium, and a thick continuous foot layer usually twice as thick as the tectum plus interstitium. Pollen data suggest two basic groupings of small-flowered genera: Group I, composed of *Dendropemon, Phthirusa* pro parte, and *Oryctanthus*; and Group II, containing *Phthirusa* pro parte, *Cladocolea, Struthanthus, Maracanthus,* and *Oryctina*. Among Group I genera, *Dendropemon* is closely linked to *Phthirusa* through the species *P. pyrifolia* and *P. platyclada*. *Oryctanthus* is a highly derived genus with only remote ties to other Group I taxa. Among Group II genera, pollen data indicate a close relationship between *Cladocolea* and the Mexican species of *Struthanthus*. Pollen characters of *Ixocactus* indicate no relationship with any small-flowered neotropical genus. Rather its pollen features are closer to those of the Eremolepidaceae and the African species of *Viscum*.

In a previous paper we detailed the pollen of the large-flowered neotropical Loranthaceae (Feuer & Kuijt, 1980). The present paper focuses on pollen characters of the small-flowered genera. Data from these two complexes will be used to analyze pollen evolution among neotropical Loranthaceae.

The small-flowered neotropical complex comprises eight genera: *Struthanthus* (ca. 50 spp.), *Cladocolea* (ca. 25 spp.), *Phthirusa* (ca. 30 spp.), *Dendropemon* (ca. 12 spp.), *Cladocolea* (ca. 25 spp.), *Phthirusa* (ca. 30 spp.) *Dendropemon* (ca. 12 spp.), *Oryctanthus* (10 spp.), *Maracanthus* (2 spp.), *Oryctina* (2 spp.), and *Ixocactus* (1 sp.). The small flower size and generally inconspicuous flower color (often pale green, buff) suggest an insect pollination mechanism, sharply contrasting with the large, showy bird-pollinated flowers of most Old and other New World mistletoes (Kuijt, 1969, 1981a).

In addition to having small flowers, the group also shows a marked tendency towards unisexual flowers and dioecism. Only three of the eight genera exhibit strictly bisexual flowers (*Oryctanthus, Dendropemon, Ixocactus*); two genera (*Phthirusa, Cladocolea*) include some species with strictly bisexual flowers and others with exclusively unisexual flowers; three genera (*Struthanthus* excluding *S. panamensis, Maracanthus, Oryctina*) demonstrate only unisexual flowers. Small flower size, the tendency towards unisexual flowers and dioecism, and an $x = 8$ chromosome number (Barlow & Wiens, 1971) together suggest an independent evolution of this group unlike Old World and other New World Loranthaceae.

MATERIALS AND METHODS

Dried flowers were collected from sheets in the following herbaria: A, CAS, F, GH, K, LEA, MO, NY, RB, S, SMU, U, UBC, UC, US, and UT. Pollen was processed according to methods out-

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TABLE 1. Summary of pollen data for small-flowered neotropical Loranthaceae.

Taxon	Size (μm)		Polarity	Shape	
	Polar	Equatorial		*Amb*	P/E
Cladocolea Tieghem (ca. 25 spp.)	13–31	23–45	isopolar	triangular to rounded convex, rarely slightly concave	0.64–0.70 oblate
Dendropemon Blume (12 spp.)	23–46	38–56	isopolar	triangular slightly to deeply concave	0.52–0.98 oblate, suboblate, rarely oblate spheroidal
Ixocactus Rizz. (1 sp.)					
I. hutchisonii Kuijt					
Cuatrecasas 23970 (F), Colombia	29.7 ± 0.13 (27.8–32)[a]	36.4 ± 0.14 (34.2–38.5)	isopolar	circular	0.82 (0.74–0.87) suboblate
Hutchison & Idrobo 3008 (F), Colombia	28.4 ± 0.09 (27.3–29.8)	32.8 ± 0.10 (31.1–34)	isopolar	circular	0.86 (0.80–0.93) suboblate
Steyermark et al. 111592 (F), Venezuela	28.1 ± 0.17 (26.9–30.1)	37.9 ± 0.11 (36.6–38.6)	isopolar	circular	0.74 (0.69–0.81) oblate
Tamayo 2526 (ILL), Venezuela	—	—	isopolar	circular	—
Maracanthus Kuijt (2 spp.)					
M. chlamydatus (Rizz.) Kuijt					
Steyermark 99522 (UC), Venezuela	17.5 ± 0.28 (14.4–19.9)	28.9 ± 0.29 (25.8–29.5)	isopolar	triangular to slightly convex	0.60 (0.46–0.71) oblate
Oryctanthus Eichler (10 spp.)	27–35	45–56	isopolar	triangular rounded convex to circular	0.56–0.70 oblate
Oryctina Tieghem (2 spp.)					
O. subaphylla Rizz.					
Anderson et al. 36949 (RB), Brazil	15.8 ± 0.11 (14.3–17.8)	24.9 ± 0.09 (23.2–26.1)	isopolar	triangular rounded convex	0.63 (0.55–0.65) oblate
Phthirusa Martius (ca. 30 spp.)	17–39	27–51	isopolar; heteropolar; isopolar-heteropolar[b]	triangular to slightly concave; trilobate (2 spp.)	0.60–0.77 oblate, suboblate, oblate spheroidal
Struthanthus Martius (ca. 50 spp.)	14–38	28–50	isopolar; heteropolar; isopolar-heteropolar	triangular to rounded convex, rarely concave	0.53–0.91 oblate to suboblate, rarely oblate spheroidal

TABLE 1. Continued.

Apertures	Sculpturing	Exine Structure
simple, compound; diplo- and synaperturate (diploparasyndemicolpate, diploparasyndemicolporate, diplosyndemicolpate, parasyncolpate)	psilate-foveolate, low profile striato-rugulate	granular/columellate, granular[c]
simple; diploaperturate (diploporate to diplobrevicolpate)	psilate-imperforate polar exine; psilate-perforate equatorial exine	columellate/baculate
4(–5)-colpate	irregular bifurcating processes and spines	—
4-colpate	irregular bifurcating processes and spines	—
(3–)4, 5-colpate	irregular bifurcating processes and spines	granular
4-colpate	irregular bifurcating processes and spines	—
syncolpate	short ridges, low profile striato-rugulate, perforate	columellate/granular
compound(?); diploaperturate (three sagittate slits at each face form the endoapertures)	psilate-imperforate	ektexinous strands traversing narrow osmiophilic zone
diplosyndemicolpate	psilate, foveolate(?), perforate(?)	—
simple; diplo-, rarely synaperturate (1 sp.) (diplosyndemicolpate, diplodemibrevicolpate, diploporate, diplo-2-demicolpate, syncolpate)	psilate-perforate; short furrows, ridges; low profile striato-rugulate	columellate/granular, columellate/baculate, columellate
simple, compound; diplo- and synaperturate (syncolpate, 3-demicolpate, diplosyndemicolpate, diploparasyndemicolpate, syncolporoidate, parasyncolporoidate, diplosyndemicolporoidate, diplosyndemicolporate, diploparasyndemicolporate)	pronounced striato-rugulate, tectate-perforate with low profile rugulae; psilate-perforate to imperforate	granular, rarely with sporadic columellae

[a] Populational mean followed by standard deviation; range in parentheses.
[b] Occurring within same population.
[c] Listed in order of dominant interstitial element.

lined in Feuer and Kuijt (1978) with the following addition. For light microscopy, acetolyzed pollen was mounted in glycerine jelly and photographed with a Nikon-UFX system at either 200× or 500× using Agfapan (ASA 25) black and white 35 mm film developed for five minutes at 68°F in Rodinal diluted 1 : 25. Specimens examined with the transmission electron microscope (TEM) are marked with an asterisk.

Aperture terms used in the present paper are briefly defined followed by a listing of all aperture types occurring among the small-flowered genera. The term: 1) demi- is used to describe a pair of apertures running perpendicularly to the equator but not confluent, thus appearing as if each set of apertures were derived by equatorial constriction and subsequent splitting; 2) diplo- is used to denote two sets of apertures (in these cases usually three to a set), each set restricted to a polar face and not continuous across the equator; 3) syn- is used to denote apertures fusing at the pole; and 4) parasyn- refers to apertures bifurcating at the pole, the bifurcations isolating a portion of exine at the center of the polar face. The following aperture combinations occur within the small-flowered complex: syncolpate (e.g., Figs. 83, 84), parasyncolpate (e.g., Figs. 68–71), diplosyndemicolpate (e.g., Fig. 74), diploparasyndemicolpate (e.g., Figs. 74–77), 2- and 3-demicolpate (e.g., Fig. 78), and compound variations (-colporoidate and colporate) of these same types, as well as diploporate (e.g., Figs. 25–29), diplobrevidemicolpate (e.g., Figs. 1, 52) and 3–4–5 colpate (e.g., Figs. 99, 100).

Pollen characters of the small-flowered genera are summarized in Table 1.

GENERIC POLLEN DESCRIPTIONS

Cladocolea Tieghem (Figs. 5–11, 68, 69, 72, 73, 87–89).

TYPE I

Exomorphology: radial symmetry, isopolar. Shape: *amb* triangular concave; oblate. Apertures: diplosyndemicolpi; colpi broad, of uniform width, with granular membranes. Sculpturing: short ridges to low profile striato-rugulae. Exine equatorially thickened near apertures.

Species and specimens examined: *Cladocolea inconspicua* (Benth.) Kuijt, *Gentry 7056* (F), Mexico (Sinaloa).

TYPE II

Exomorphology: radial symmetry, isopolar. Shape: *amb* triangular to rounded convex; oblate. Apertures: diploparasyndemicolpori; ectoapertures shallow colpi delimiting a prominent round or triangular apocolpium; endoapertures ranging from U-shaped to elliptical slits to large circular subsurface thinnings lying perpendicular to and in midregion of colpi on polar faces. Sculpturing: psilate-foveolate to shallow striato-rugulate. Equatorial exine thickened near apertures.

Species and specimens examined: *Cladocolea andrieuxii* Tieghem, *Pringle 10244* (SMU), Mexico (Oaxaca); *C. loniceroides* (Tieghem) Kuijt, *Hinton 3796* (UC), Mexico (Mexico), *Hinton 10500* (GH), Mexico (Guerrero); *C. microphylla* (H.B.K.) Kuijt, **Pringle 4369* (UC), Mexico (Jalisco).

TYPE III

Exomorphology: radial symmetry, isopolar. Shape: *amb* triangular to slightly rounded convex; oblate. Apertures: parasyncolpi; colpi delimiting a small apocolpium. Sculpturing: psilate-foveolate to shallow striato-rugulate. Exine evenly thickened at equator.

Species and specimens examined: *Cladocolea*

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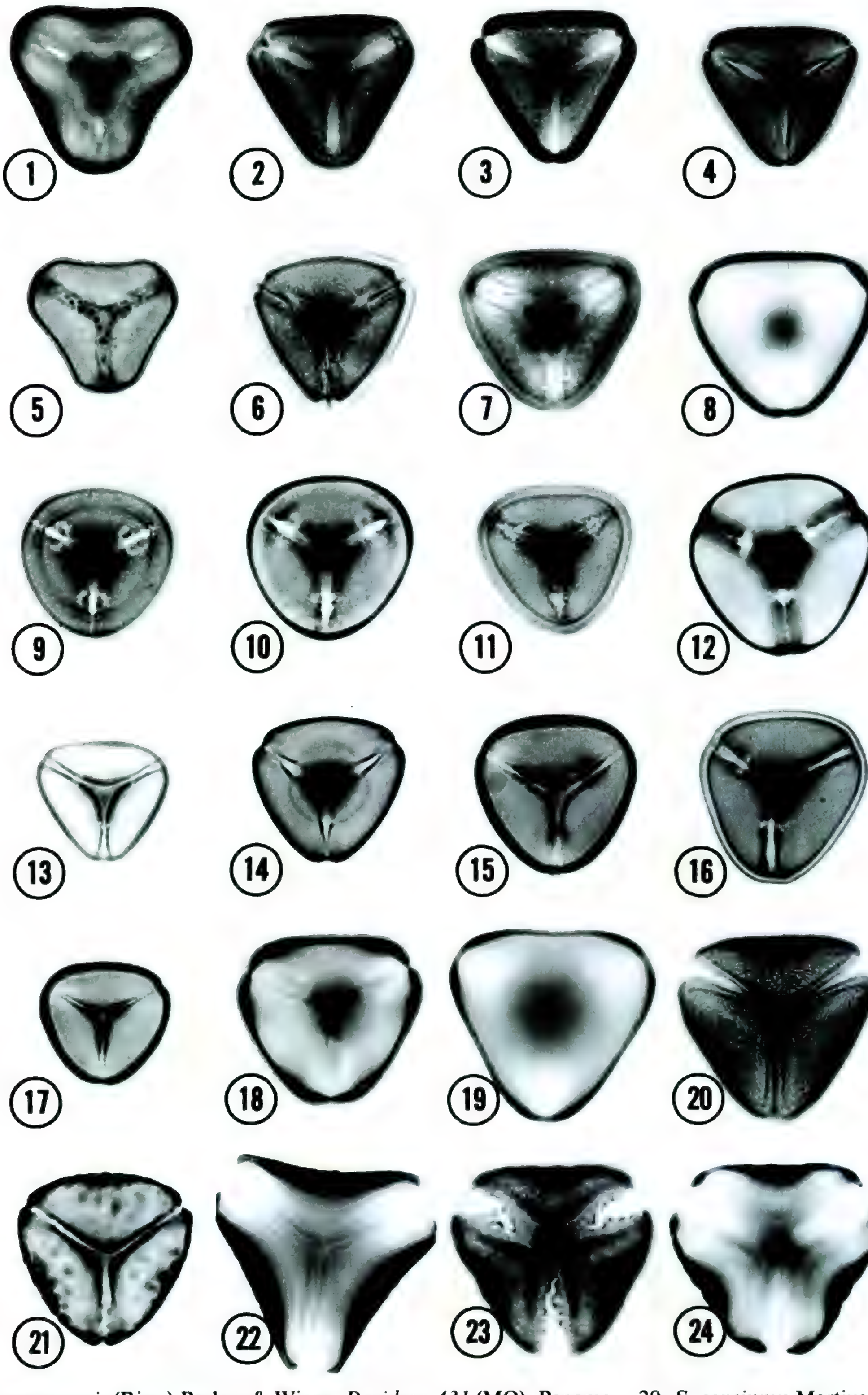
FIGURES 1–24. Polar views of *Phthirusa* spp. (1–3), *Maracanthus chlamydatus* Rizz. (4), *Cladocolea* spp. (5–11), *Oryctina subaphylla* Rizz. (17), and *Struthanthus* spp. (12–16, 18–24). All light micrographs, ×700.—1. *P. lepidobotrys* Eichler, Jamaica.—2. *P. retroflexa* (Ruíz & Pavón) Kuijt, *Nee & Hansen 14038* (F), Panama. Polar face with protruding colpal margins.—3. *P. retroflexa* (Ruíz & Pavón) Kuijt, *Nee & Hansen 14038* (F), Panama. Opposite polar face of same grain.—4. Focal plane slightly below apocolpial exine.—5. *C. inconspicua* (Benth.) Kuijt.—6. *C. pringlei* Kuijt, *Pringle 4697* (UC), Mexico.—7. *C. andrieuxii* Teighem. Focal plane at the level of the endoapertures.—8. *C. andrieuxii* Tieghem. Focal plane at the equator. Note prominently thickened exine at the apertures.—9. *C. microphylla* (H.B.K.) Kuijt. Grain with U-shaped endoapertures.—10. *C. microphylla* (H.B.K.) Kuijt. Grain with elliptical endoapertures.—11. *C. loniceroides* (Tieghem) Kuijt, *Hinton 10500* (GH), Mexico.—12. *S. densiflorus* Standley.—13. *S. leptostachyus* (H.B.K.) G. Don, *Skutch 2618* (A), Costa Rica. Grain with barely discernible endoapertures.—14. *S. costaricensis* Standley.—15. *S. palmeri* Kuijt.—16. *S. belizensis* Lundell.—17. Focal plane at apocolpium.—18. *S. oerstedii* Standley, *Barlow 1443* (UC), Costa Rica.—



19. *S. panamensis* (Rizz.) Barlow & Wiens, *Davidson 431* (MO), Panama.—20. *S. concinnus* Martius.—21. *S. uraguensis* (Hook. f. & Arnell) G. Don, *Hatschbach 17641* (UC), Brazil.—22. *S. uraguensis* var. *brevipedunculata* Chodat & Hassler.—23. *S. vulgaris* Martius. Focal plane at the apocolpium.—24. *S. vulgaris* Martius. Focal plane at the equator.

glauca Kuijt, *Borys et al. 6* (LEA), Mexico (Puebla); *C. grahamii* (Benth.) Tieghem, *Hinton 10149* (GH), Mexico (Oaxaca), *Pringle 6987* (F), Mexico (Mexico); *C. harlingii* Kuijt, **Harling 6094* (S), Ecuador, *Wiens 3781* (LEA, UT), Ecuador, *Wiens 3800* (UT), Ecuador; *C. pringlei* Kuijt, *Breckon & Breckon 803* (GH), Mexico (Oaxaca), *Conzatti 1899* (F), Mexico (Oaxaca), *Pringle 4697* (UC), Mexico (Oaxaca).

TYPE IV

Exomorphology: radial symmetry, isopolar. Shape: *amb* triangular; oblate. Apertures: diplosyndemicolpi. Sculpturing: short ridges to low profile rugulae. Polar faces exhibiting central circular thickening; equatorial exine evenly thickened.

Species and specimens examined: *Cladocolea oligantha* (Standley & Steyerm.) Kuijt, *Rzedowski 22674* (CAS), Mexico (Guerrero).

Endomorphology: ektexine and endexine present. Ektexine organized into tectum, interstitium, and foot layer. Tectum evenly thickened, occasionally foveolate, rarely perforate. Interstitium narrow, typically sparse and finely granulate with short, irregularly shaped columellae sometimes present; in *C. harlingii* interstitium characterized by short projections pendent from tectum or projecting upwards from foot layer, these intercalated between horizontally coalescing ektexinous strands. Foot layer with typically smooth upper surface and shallowly scalloped lower edge. Endexine absent in interapertural equatorial regions, present in central regions of polar faces and regions adjacent to colpi; polar endexine bistratified with upper zone adjacent to foot layer characterized by numerous osmiophilic channels, basal zone slightly thicker, homogeneous; endexine near apertures irregularly thickened, disrupted by numerous small gaps; apertural endexine thin, disrupted, loosely organized into small lamellae or more granular strands.

Tectum/Equatorial interstitium//Foot layer: 1:2.

Species and specimens examined: all species listed under exomorphology that are marked by an asterisk.

Dendropemon Blume (Figs. 25, 26, 29, 32, 36–40).

Exomorphology: radial symmetry, isopolar. Shape: *amb* triangular slightly concave to trilobate deeply concave; oblate to suboblate or oblate spheroidal. Grains diploaperturate. Apertures: ranging from elliptical pores to broad brevicolpi, typically restricted to tips of pollen lobes and encircled by subsurface thickened exine continuous with subsurface triradiate polar thickening, membranes disrupted. Sculpturing: psilate imperforate at the polar faces and tips of pollen lobes, exine minutely perforate in interapertural equatorial areas. Exine with triradiate thickening at polar faces and equatorially thickened lobes.

Endomorphology: ektexine and endexine present. Differences in interapertural equatorial, lobar equatorial, and polar ektexine organizations. Interapertural equatorial ektexine organized into tectum, columellate/baculate interstitium, and foot layer. Tectum with narrow perforations. Interstitium exhibiting short, basally thickened columellae interspersed among rounded baculae pendent from tectum or extending up from foot layer. Foot layer thick with smooth upper and lower surfaces. Lobar equatorial ektexine organized into large irregularly shaped ektexinous masses pendent from thick imperforate tectum. Polar ektexine thicker than equatorial ektexine, bistratified; upper stratum imperforate with smooth upper surface; lower stratum significantly thicker, upper surface slightly granular; strata separated by a narrow, poorly defined zone often filled with granules and occasionally bridged by extremely narrow short columellae. Endexine ranging from thick, continuous and coarsely granular to thin and locally absent beneath the

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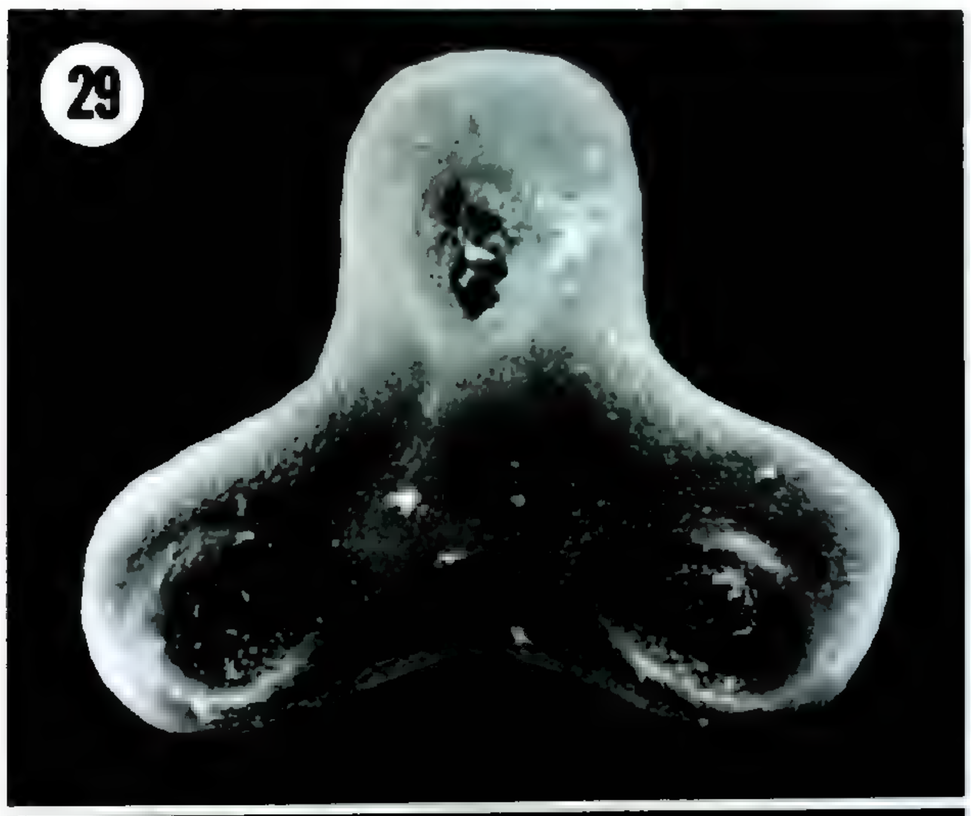
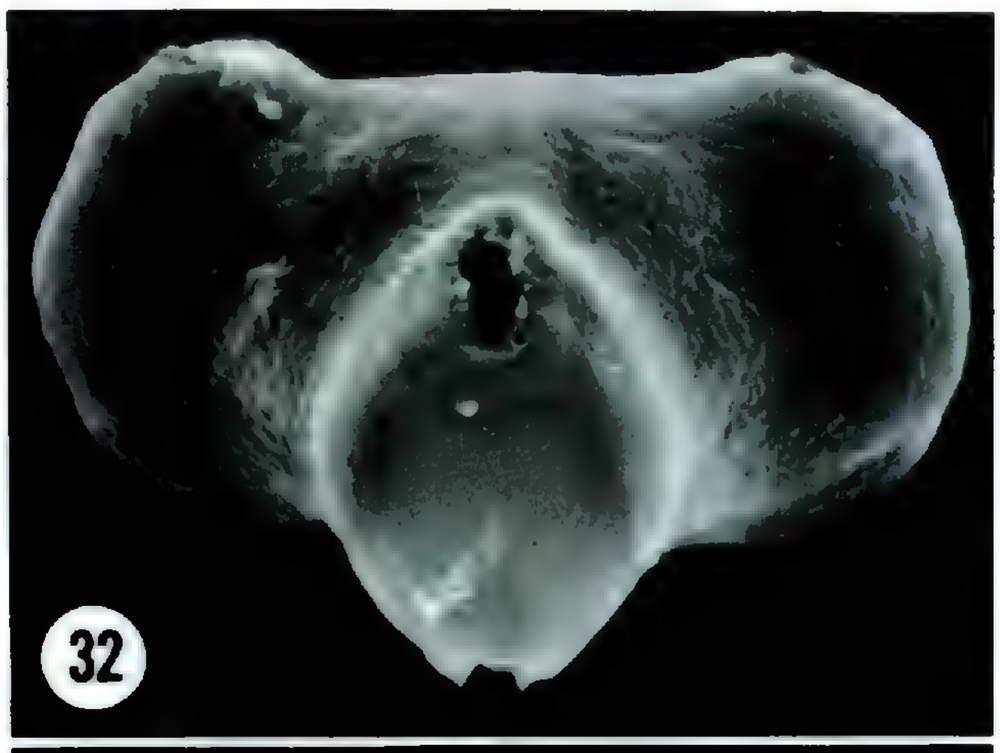
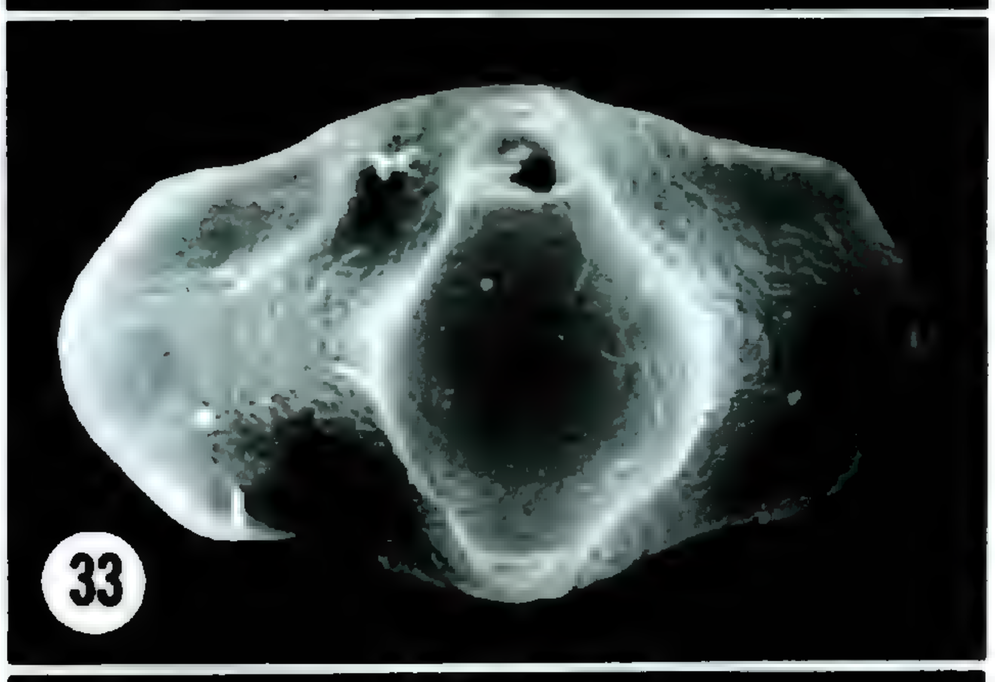
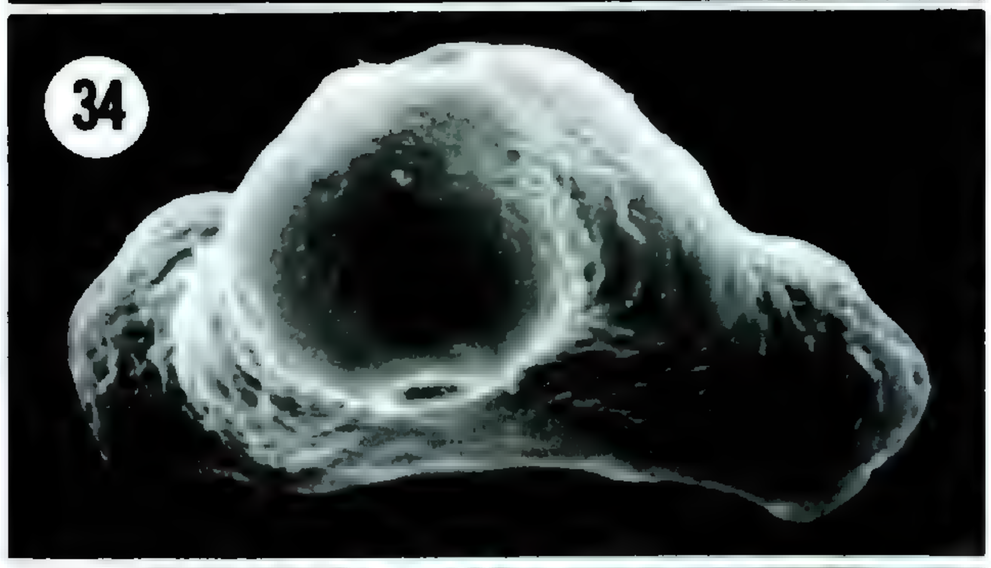
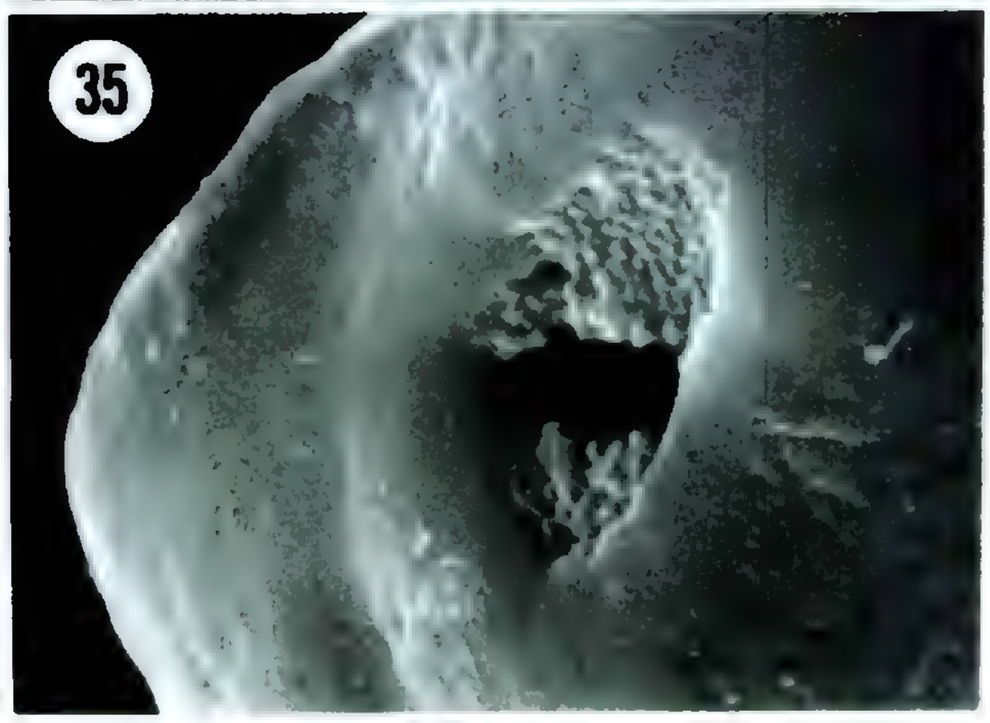
FIGURES 25–35. Comparisons between *Dendropemon* Blume and *Phthirusa* Martius (LM, SEM). 25, 26, 29, 32. *Dendropemon* spp. 27, 28, 30, 31, 33–35. *Phthirusa* spp.—25. *D. uniflorus* Steud., *Leonard et al. 15026* (UC), Haiti. Focal plane just below the apocolpial exine, ×500.—26. *D. uniflorus* Steud., *Leonard et al. 15026* (UC), Haiti. Light micrograph with focal plane at equator, ×500.—27. *P. platyclada* Ule. Light micrograph with focal plane just below the apocolpial exine, ×500.—28. *P. pyrifolia* (H.B.K.) Eichler, *Greenhouse-collected Kuijt*, Costa Rica. Light micrograph with focal plane just below the apocolpial exine, ×500.—29. *D. purpureus* Krug & Urban, *Liogier 15253* (F), Hispaniola. Polar view, ×1,330.—30. *P. platyclada* Ule. Polar view, ×2,000.—31. *P. pyrifolia* (H.B.K.) Eichler, *Greenhouse-collected Kuijt*, Costa Rica. Polar view, ×2,080.—32. *D. constantiae*



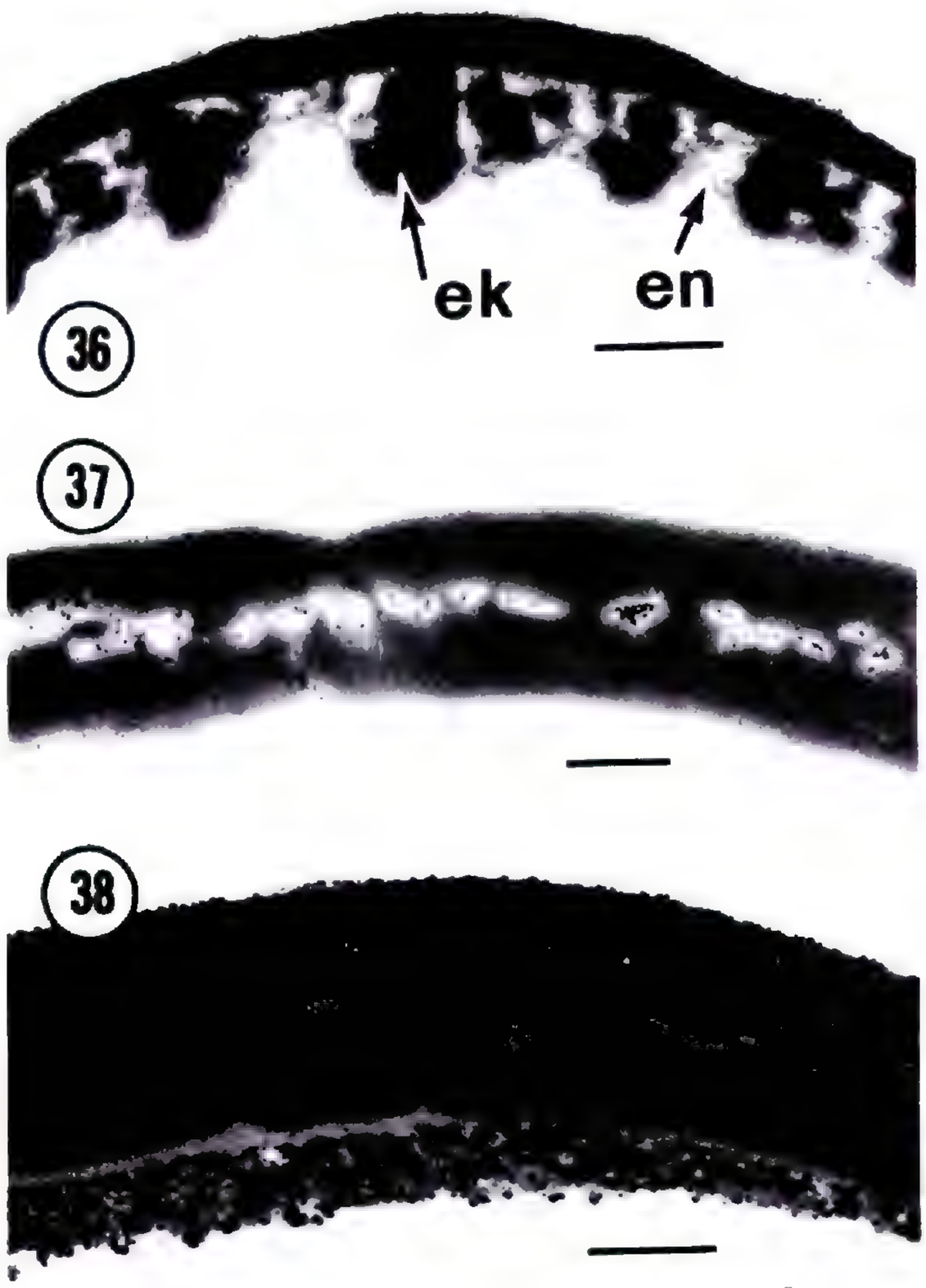








Krug & Urban. Equatorial view, ×1,400.—33. *P. platyclada* Ule. Equatorial view, ×2,000.—34. *P. pyrifolia* (H.B.K.) Eichler, *Greenhouse-collected Kuijt*, Costa Rica. Equatorial view, ×2,100.—35. *P. pyrifolia* (H.B.K.) Eichler, *Greenhouse-collected Kuijt*, Costa Rica. Detail of aperture. Note the symmetrical break in the aperture membrane, ×6,000.



FIGURES 36–41. Ultrastructural comparisons between *Dendropemon* Blume (36–40) and *Phthirusa* Martius (41) (TEM).—36. *D. bahamensis* Britton. Detail of lobar exine. The ektexine (ek) is organized into irregularly shaped pendent structures connected by thin strands of endexine (en), ×9,000.—37. *D. bahamensis* Britton. Detail of polar exine, ×7,500.—38. *D. pycnophyllus* Krug & Urban. Detail of polar exine exhibiting well-developed endexine, ×9,750.—39. *D. bahamensis* Britton. Section through polar thickening (pt) and adjacent lobe (l), ×2,400.—40. *D. bahamensis* Britton. Detail of equatorial exine revealing columellate/baculate interstitium and narrow stratum of endexine, ×16,100.—41. *P. platyclada* Ule. Ektexine composed of sporadic, irregularly shaped columellae and irregularly thickened foot layer, ×11,000. All lines in micrographs equal 1 μm.

polar faces, thinning in lobar regions present here as thin strands connecting lower surfaces of irregularly shaped ektexinous segments, typically absent in interapertural equatorial areas, but in some species (e.g., *D. bahamensis*) present as a thin continuous stratum.

Tectum/Equatorial interstitium//Foot layer: 1:3 to 2:1.

Species and specimens examined: *Dendropemon bahamensis* Britton, **Popenoe 5* (A), Bahama Is.; *D. caribaeus* Krug & Urban, *Britton et al. 45* (MO), West Indies (St. Thomas), *Duss 2419* (GH), West Indies (Guadeloupe); *D. constantiae* Krug & Urban, *Cicero et al. 6040* (MO), Hispaniola; *D. emarginatus* Steud., *Correll 44095* (MO), Bahama Is., *Correll & Correll 47922* (F), Bahama Is. (Great Exuma), *Smith et al. 3345* (F), Cuba; *D. pauciflora* Tieghem, *Maxon 8761* (GH), Jamaica; *D. picardiae* Krug & Urban, *Ekman H12947* (GH), Hispaniola; *D. purpureus* Krug & Urban, *Liogier 15253* (F), Hispaniola, *Wilson 7647* (F), Bahama Is. (Caicos Is.); *D. pycnophyllus* Krug & Urban, **Liogier 17966* (F), Hispaniola; *D. rostratus* Urban, *Ekman H10199* (GH), Hispaniola; *D. uniflorus* Steud., *Leonard & Leonard 12470* (MO), Haiti (Tortue Is.), *Leonard et al. 15026* (UC), Haiti.

Ixocactus Rizz. (Figs. 98–104).

Exomorphology: radial symmetry, isopolar. Shape: *amb* circular; oblate, suboblate rarely oblate spheroidal. Apertures: colpi, varying in number within and among populations from (3 to) 4 to 5 colpate. Sculpturing: densely clustered blunt-tipped spines and more irregularly shaped often bifurcating segments. Exine thickest in interapertural equatorial regions thinning slightly near apertures.

Endomorphology: ektexine and endexine present. Non-apertural ektexine exhibiting two types of organization on same grain: Type I with bistratified ektexine; upper stratum composed of variably thick, solid, broad, frequently irregularly branching segments, the branches sometimes elaborated into blunt-tipped spines; basal stratum solid, variably thick with granular upper and slightly scalloped lower surfaces; both strata separated by extremely narrow, sparsely granular interstitium; and Type II, composed of a basically single stratum of ektexine similar in structure to Type I resting on small, highly channeled, loosely aggregated ektexinous segments randomly attached to lower surface of upper ektexine. Endexine, beneath Type I ektexine, solid, continuous irregularly thickened but, beneath Type II, organized into loosely arranged, small isolated segments attached to ektexine.

Tectum/Equatorial interstitium//Foot layer: 4:1 (Type I ektexine).

Species and specimens examined: *Ixocactus hutchisonii* Kuijt, *Cuatrecasas 23970* (F), Colombia, **Hutchison & Idrobo 3008* (F), Colombia, *Steyermark et al. 111592* (F), Venezuela, *Tamayo 2526* (ILL), Venezuela.

Maracanthus Kuijt (Figs. 4, 50, 53, 67).

Exomorphology: radial symmetry, isopolar. Shape: *amb* triangular to slightly convex; oblate. Apertures: syncolpi; colpi narrow, shallow, slightly broader on the polar faces, narrowing at the equator. Sculpturing: short ridges, low profile striato-rugulae, exine foveolate and perforate, these most common in interapertural equatorial areas; polar faces psilate, imperforate. Exine thickened in a circular configuration directly at the center of the polar faces.

Endomorphology: ektexine and endexine present. Slight structural differences between equatorial and polar ektexine. Equatorial ektexine organized into tectum, columellate/granular interstitium, and foot layer. Tectum evenly thickened, foveolate, perforate, and channeled, the latter thin and not continuous through tectum. Interstitium clearly defined, composed of irregularly thickened columellae interspersed among baculae and baculae-like structures, the latter pendent from the tectum and surrounded by a finely granular matrix. Foot layer discontinuous in small localized areas, extremely thick, with a smooth upper surface and sporadically scalloped lower edge. Polar ektexine thinner than equatorial ektexine, organized into a thick, rarely perforate or foveolate tectum and poorly delimited, predominantly granular interstitium exhibiting a few short, irregularly thickened columellae. Foot layer thinner than that in equatorial areas, irregularly thickened, highly scalloped lower edge. Endexine present at the polar faces and beneath apertures but typically absent in equatorial areas though sometimes filling the small gaps in lower edge of foot layer.

Tectum/Equatorial interstitium//Foot layer: 1:2.

Species and specimens examined: *Maracanthus chlamydatus* (Rizz.) Kuijt, **Steyermark 99522* (UC), Venezuela.

Oryctanthus Eichler (Figs. 42–49).

Exomorphology: radial symmetry, isopolar. Shape: *amb* circular; polar face characterized by three circular depressions each bounded by a narrow, raised rounded ridge, the ridges confluent at the center of the polar face forming a triradiate configuration; equatorial ridge also present; oblate. Grains compound diploaperturate. Apertures: ectoaperture a short, elliptical colpus; endoaperture a sagittate opening; apertures placed 120° apart at the tips of the triradiate central ridge and between the ridges which encircle each of the polar depressions. Sculpturing: psilate, imperforate with loosely granular exine occasionally present in depressed circular polar areas. Exine thickened in equatorial areas aligned with apertures and in the center of each of the three circular polar depressions.

Endomorphology: ektexine and endexine present. Ektexine typically bistratified, organized into upper and lower solid strata separated by a narrow, highly undulate, osmiophilic layer; strata connected by numerous, sporadic, extremely short strands of ektexine; equatorial ridges formed by the outward looping and subsequent appression or fusion of the bistratified ektexine; ektexinous strata at the base of the polar depressions separated by a broad, coarsely granular zone, the upper stratum giving rise to a thin network of fine, randomly anastomosing granules. Endexine not continuous around grain, absent beneath polar depressions but prominent and irregularly thickened directly beneath equatorial ridges, thin and locally discontinuous in nondepressed polar areas; apertural endexine thin, loosely granular.

Tectum/Equatorial interstitium//Foot layer: 1:1.

Species and specimens examined: *Oryctanthus alveolatus* (H.B.K.) Kuijt, *Steyermark 87665* (GH), Venezuela; *O. asplundii* Kuijt, *Prance et al. 7284* (UT), Brazil; *O. cordifolius* (Presl) Urban, *Fryxell 683a* (UT), Mexico, **Kuijt 2571* (UBC), Costa Rica; *O. florulentus* (Rich.) Urban, *Broadway 681* (GH), French Guiana, *Wiens 3741* (UT), Ecuador; *O. occidentalis* (L.) Eichler, *Kuijt 2440* (UBC), Costa Rica; *O. phanerolomus* (Standley) Kuijt, *Gentle 1405* (GH), British Honduras; *O. spicatus* (Jacq.) Eichler, **Killip & Smith 16807* (GH), Colombia.

Oryctina Tieghem (Fig. 17).

Exomorphology: radial symmetry, isopolar. Shape: *amb* triangular slightly convex; oblate. Apertures: diplosyndemicolpi; colpal membranes slightly disrupted on polar faces approaching equator, demicolpi separated by extremely narrow bridge of exine at equator. Sculpturing: psilate, foveolate and perforate(?). Exine evenly thickened at equator, slightly thicker along colpal margins at centers of polar faces.

Endomorphology: not examined.

Species and specimens examined: *Oryctina subaphylla* Rizz., *Anderson, Stieber & Kirkbride 36949* (RB), Brazil.

Phthirusa Martius (Figs. 1–3, 27, 28, 30, 31, 33–35, 41, 51, 52, 54–56).

TYPE I

Exomorphology: similar to *Dendropemon* spp. with *Phthirusa* species differing by smaller grain size.

Endomorphology: similar to that of *Dendropemon* spp., particularly *D. bahamensis.*

Tectum/Equatorial interstitium//Foot layer: 1:1.66.

Species and specimens examined: *Phthirusa pyrifolia* (H.B.K.) Eichler, *Croat 18038* (LEA), Peru, *Revilla 2173* (MO), Peru, **Greenhouse* (*collected Kuijt*), Costa Rica; *P. platyclada* Ule, **Asplund 12376* (S), Peru.

TYPE II

Exomorphology: radial symmetry, iso- and/or heteropolar. Shape: *amb* triangular to slightly concave; oblate to suboblate. Differences in polarity, aperture types and sculpturing distinguish the following subtypes:

Subtype A. Grains isopolar. Apertures: dip-

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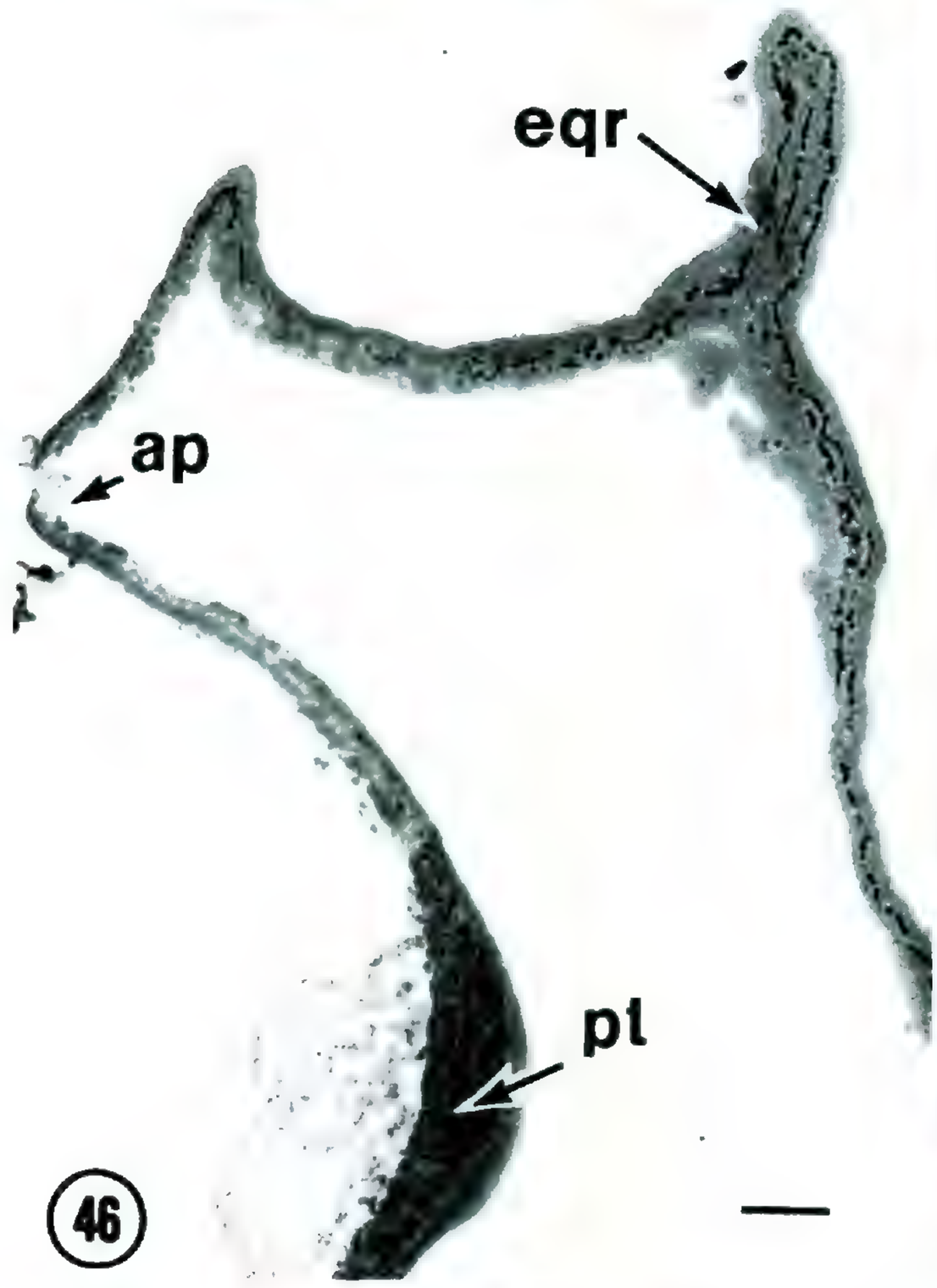
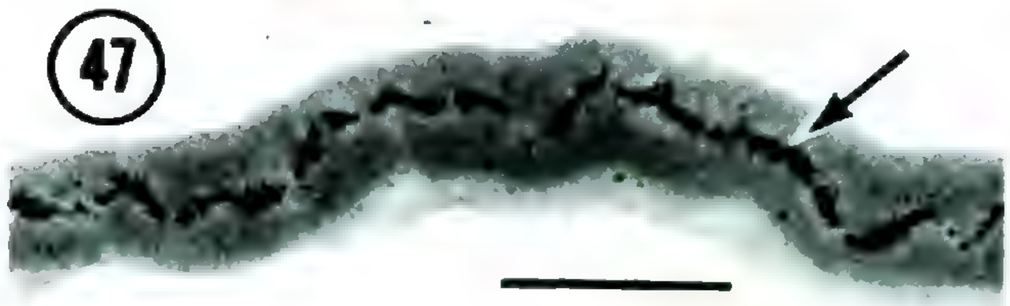
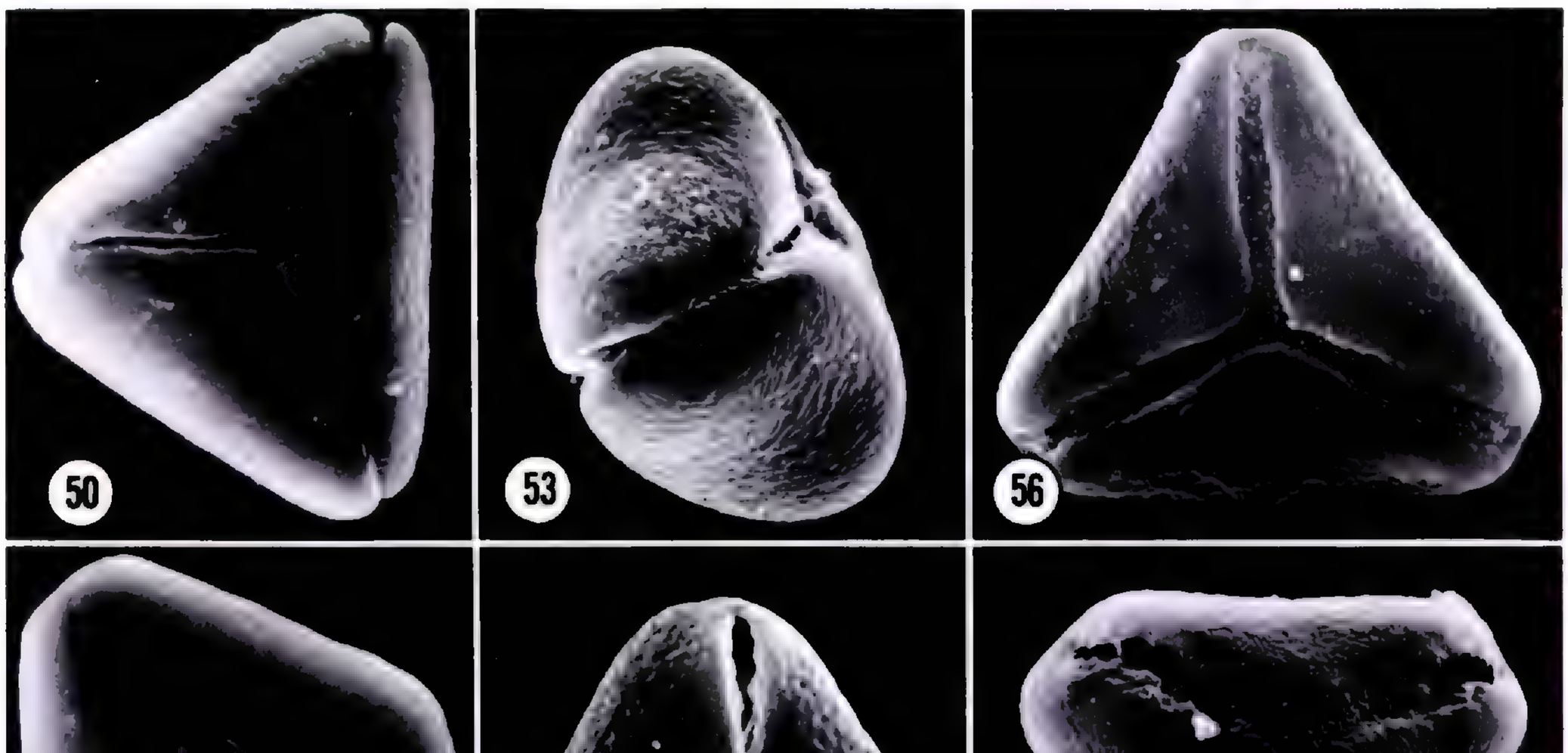
FIGURES 42–49. *Oryctanthus* Eichler. 42, 43. *O. spicatus* (Jacq.) Eichler. 44–49. *O. cordifolius* (Presl) Urban, *Kuijt 2571* (UBC), Costa Rica.—42. Light micrograph (LM) with focal plane at the level of the triradiate polar thickening revealing three sagittate apertures, ×500.—43. LM with focal plane at the equator clearly revealing central polar thickenings in each of the polar depressions (arrowhead), ×500.—44. Polar view. The sagittate apertures, though prominent in the LM, are barely discernible in the SEM, ×1,340.—45. Oblique equatorial view revealing equatorial ridge and raised polar thickening, ×1,535.—46. Thin section perpendicular to polar





face through a polar depression including its central thickening (pt), an adjacent aperture (ap), and equatorial ridge (eqr), ×6,000.—47. Detail of polar exine. Narrow bands of ektexine (arrow) connect the ektexinous strata, ×14,000.—48. Detail of polar thickening which lies at the center of each of the polar depressions. In some species a finely granular matrix is attached to the tectum, ×8,700.—49. Detail of equatorial ridge adjacent to polar depression revealing looped appressed ektexine and thickened endexine (en), ×8,700. All lines in micrographs equal 1 μm.



FIGURES 50–58. Comparisons between *Maracanthus* Kuijt and *Phthirusa* Martius (SEM). 50, 53. *Maracanthus chlamydatus* (Rizz.) Kuijt. 51, 52, 54–58 *Phthirusa* spp.—50. Polar view of syncolpate grain, ×1,250.—51. *P. coarctata* A. C. Smith. Polar view of diplosyndemicolpate grain (Type II-A), ×1,330.—52. *P. lepidobotrys* Eichler. Polar view of 3-diplodemibrevicolpate grain (Type II-B3), ×1,250.—53. Oblique equatorial view, ×1,250.—54. *P. micrantha* Eichler. Polar view of diplosyndemicolpate grain (Type II-A), ×1,500.—55. *P. magdalenae* (Cham. & Schldl.) Eichler. Polar view showing protruding colpal margin of diplosyndemicolpate grain (Type II-C1), ×1,250.—56. *P. ovata* (Pohl) Eichler. Polar view of diplosyndemicolpate grain (Type II-B2), ×1,250.—57. *P. theloneura* Eichler. Diplosyndemicolpate grain (Type II-C2). Polar view, ×1,200.—58. *P. theloneura* Eichler. Equatorial view, ×1,200.

losyndemicolpi; colpi terminating subequatorially, broadening near equator with membranes frequently disrupted. Sculpturing: psilate, exine perforate and foveolate, these occurring randomly, tending to be more numerous in equatorial than polar areas.

Species and specimens examined: *Phthirusa coarctata* A. C. Smith, *Smith 2204* (U), British Guiana; *P. micrantha* Eichler, *Carreira 31* (RB), Brazil, *Spruce 1782* (K), Brazil; *P. monetaria* Sandw., *Forest Dept. #2942* (K), British Guiana; *P. sandwithii* Maguire, *Sandwith 1404* (K), British Guiana.

Subtype B. Grains isopolar. Sculpturing: numerous randomly arranged short furrows and perforations frequently surrounded by low coarse ridges. Exine bordering apertures and apocolpium (when present), psilate, imperforate. Differences in apertures distinguish the following species:

B1. Apertures: syncolpi.

Species and specimens examined: *Phthirusa squamulosa* Klotzsch ex Eichler, **Maguire & Stahl 24972* (F), Surinam.

B2. Apertures: diplosyndemicolpi; colpi narrow becoming slightly broader near equator.

Species and specimens examined: *Phthirusa ovata* (Pohl) Eichler, **Irwin et al. 7974* (UC), Brazil; *P. rufa* var. *tentaculifera* Rizz., *Ducke 26* (RB), Brazil, **Ducke 1919* (K), Brazil.

B3. Apertures: 3-diplobrevidemicolpi; colpi displaced entirely onto polar faces, forming large psilate, imperforate apocolpia.

Species and specimens examined: *Phthirusa lepidobotrys* Eichler, **Nichols s.n.* (K), Jamaica.

Subtype C. Grains iso- and/or heteropolar with respect to apertures. Isopolar grains diplosyndemicolpate. Heteropolar grains with one polar face syndemicolpate, opposite face 3-demicolpate, rarely 2-demicolpate, the latter through extrusion of a colpal margin and subsequent fusion with opposite colpal border. Sculpturing: ranging from ridges to striato-rugulae on same grain; ridges short, undulating, largely confined to midequatorial regions; striato-rugulae in low relief, largely confined to areas bordering psilate margins of colpi. Differences in polarity distinguish the following species:

C1. Grains isopolar and heteropolar within populations.

Species and specimens examined: *Phthirusa lobaterae* Ferrari, *Steyermark et al. 120118* (MO), Venezuela; *P. magdalenae* (Cham. & Schldl.) Eichler, **Langenheim 3101* (UC), Colombia; *P. retroflexa* (Ruíz & Pavón) Kuijt, *Gentry & Berry 14667* (MO), Venezuela, **Nee & Hansen 14038* (F), Panama.

C2. Grains isopolar.

Species and specimens examined: *Phthirusa krukovii* A. C. Smith, *Krukoff 5938* (A), Brazil; *P. retroflexa* (Ruíz & Pavón) Kuijt, **Allen 80* (MO), Colombia; *P. theloneura* Eichler, **Spruce s.n.* (K), Brazil.

C3. Grains heteropolar.

Species and specimens examined: *Phthirusa angulata* Krause, *Maguire & Fanshawe s.n.* (K), British Guiana; *P. jamaicensis* Krug & Urban, *Purdie* (K), Jamaica; *P. stenophylla* Eichler, *Spruce 3307* (GH), Brazil.

Endomorphology: exine organization similar to that of *Maracanthus*. *Phthirusa* species differ in the following characters: 1) tectum ranges from highly to rarely perforate; 2) a strictly columellate interstitium exists in several species where the columellae, though small and sporadic, are not associated with granular elements; and 3) continuous foot layer.

Tectum/Equatorial interstitium//Foot layer: 1:1.33.

Species and specimens examined: all species listed under exomorphology that are marked by an asterisk.

Struthanthus Martius (Figs. 12–16, 18–24, 70, 71, 74–86, 90–97).

TYPE I

Exomorphology: radial symmetry, grains isopolar or heteropolar. Shape: *amb* triangular to triangular convex; oblate, suboblate, rarely oblate spheroidal. Apertures: compound. Ectoaperture a smooth-margined colpus. Endoaperture ranging from a small well-developed rectangular to elliptical slit to an obscurely margined area lying perpendicular to and in midregion of ectocolpus on the polar faces. Sculpturing: psilate-imperforate to perforate or rarely low profile striato-rugulae. Differences in apertures and polarity distinguish the following subtypes:

Subtype A. Endoapertures well developed.

A1. Grains isopolar; diplosyndemicolporate.

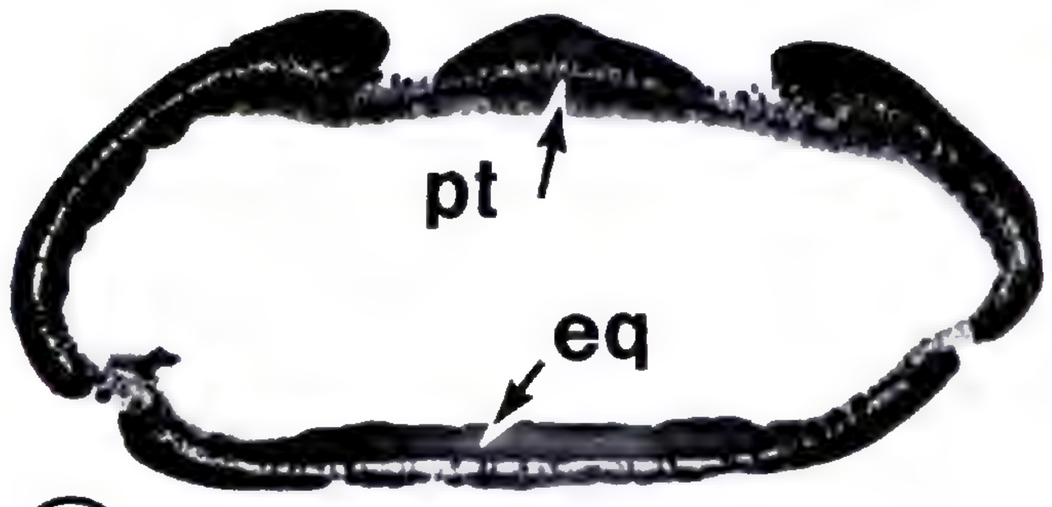
Species and specimens examined: *Struthanthus belizensis* Lundell, **Lundell* 6273 (SMU), British Honduras; *S. densiflorus* Standley, **Moore & Wood 3666* (UC), Mexico (Hidalgo); *S. leptostachyus* (H.B.K.) G. Don, *Mori & Kallunki 5308* (LEA), Panama; *S. quercicola* (Cham. & Schldl.) Blume, **Barlow 1429* (UT), Costa Rica, *Chrysler 5031* (F), Costa Rica, *Smith A519, 11479* (F), Costa Rica; *S. rotundatus* Rizz., *Lewis et al. 600* (MO), Panama, *Nee 10651, 14137* (MO), Panama.

A2. Grains heteropolar with respect to apertures; diploaperturate: one polar face parasyndemicolporate, opposite face either syndemicolporate or 3-demicolporate.

Species and specimens examined: *Struthanthus dichotrianthus* Eichler, **Smith 1279* (MO), Colombia, *Woytkowski 8269* (UC), Peru.

A3. Grains isopolar; syncolporate.

Species and specimens examined: *Struthanthus orbicularis* (H.B.K.) Blume, *Barlow 1507* (UT), Costa Rica, **Burger & Baker 10095* (F), Costa Rica; *Williams 16049* (F), Costa Rica; *Ortiz 798* (UC), Guatemala.



FIGURES 59–67. Ultrastructural comparisons between *Phthirusa* Martius and *Maracanthus* Kuijt (TEM). 59–62. *Phthirusa ovata* (Pohl) Eichler. 63–66. *Phthirusa* spp. 67. *Maracanthus chlamydatus* (Rizz.) Kuijt.—59. Section through equator, ×4,500.—60. Section through polar thickening (pt) at the apocolpium and opposite equatorial exine (eq), ×3,200.—61. Detail of equatorial exine revealing short, sparsely distributed columellae, ×11,250.—62. Detail of apocolpial exine (ac), ×6,000.—63. *P. theloneura* Eichler. Detail of equatorial exine,

Subtype B. Endoapertures poorly developed with often obscure margins.

B1. Grains isopolar; diplosyndemicolporoidate.

Species and specimens examined: *Struthanthus escuintlensis* Lundell, *Matuda 4185* (A), Mexico (Chiapas); *S. leptostachyus* (H.B.K.) G. Don, *Skutch 2618* (A, US), Costa Rica; *S. macrostachyus* Lundell, *Breedlove 25943* (MO), Mexico (Chiapas), *Janzen s.n.* acc. #303522 (UC), Mexico (Oaxaca).

B2. Grains heteropolar; diploaperturate; one polar face parasyndemicolporoidate, opposite face either syndemicolporoidate or demicolporoidate.

Species and specimens examined: *Struthanthus marginatus* (Desr.) Blume, **Barlow 1420* (UC), Costa Rica, *Thorne & Lathrop 40173* (UT), Mexico (Chiapas).

B3. Grains heteropolar; synaperturate, one polar face parasyncolporoidate, opposite face syncolporoidate.

Species and specimens examined: *Struthanthus deppeanus* (Cham. & Schldl.) Blume, **Balls 4340* (A), Mexico (Veracruz).

TYPE II

Exomorphology: radial symmetry, grains isopolar or heteropolar, rarely subisopolar. Shape: oblate, suboblate, rarely oblate spheroidal. Apertures simple, diplo- or synaperturate, the colpi sometimes broader in midregions of polar faces narrowing at the equator. Sculpturing: psilate-perforate and/or foveolate, rarely low profile striato-rugulae. Differences in *amb,* aperture characters, and patterns of exine thickening distinguish the following species:

Subtype A. Grains isopolar; triangular to rounded convex; syncolpate; exine evenly thickened around grain.

Species and specimens examined: *Struthanthus costaricensis* Standley, **Barlow 1402* (UC, UT), Costa Rica; *S. interruptus* (H.B.K.) Blume, *Nagel 8026* (GH), Mexico (Morelos).

Subtype B. Grains isopolar rarely subisopolar (*S. cassythoides*) the latter with one polar face less rounded convex than opposite face; triangular rounded convex; diploparasyndemicolpate; exine evenly thickened around equator but thinning beneath colpi at periphery of polar faces.

Species and specimens examined: *Struthanthus cassythoides* Millsp. ex Standley, *Gentle 1660* (UC), British Honduras; *S. palmeri* Kuijt, **LeSueur 1071* (F, GH), Mexico (Chihuahua).

Subtype C. Grains isopolar; triangular to concave; diplosyndemicolpate; exine thinning in midequatorial regions and beneath colpi in peripheral regions of polar faces, thickening near apertures in equatorial areas and at centers of polar faces.

Species and specimens examined: *Struthanthus oerstedii* Standley, *Barlow 1443* (UC, UT), Costa Rica, *Howell 10243* (F), Costa Rica, *Utley et al. 2701* (F), Costa Rica; *S. panamensis* (Rizz.) Barlow & Wiens, **Davidson 431* (MO, US), Panama, *Luteyn 3786* (F), Panama.

Endomorphology: ektexine and endexine present. Ektexine organized into tectum, interstitium, and foot layer. Tectum regularly thickened, rarely perforate. Interstitium narrow, poorly defined, coarsely granular occasionally exhibiting irregularly shaped columellae and columellae-like structures. Foot layer continuous, with an uneven upper surface and typically smooth lower surface showing an occasional small gap. Endexine present at polar faces and beneath apertures, rarely present in interapertural areas and then only filling gaps in lower edge of foot layer; polar endexine slightly thicker than apertural endexine, homogeneous.

Tectum/Equatorial interstitium//Foot layer: 1 : 1.

Species and specimens examined: all species marked by an asterisk and exhibiting Types I and II exomorphologies, excluding *S. panamensis.*

Endomorphology: ektexine and endexine present. Ektexine organized into tectum, interstitium, and foot layer. Tectum irregularly thick-

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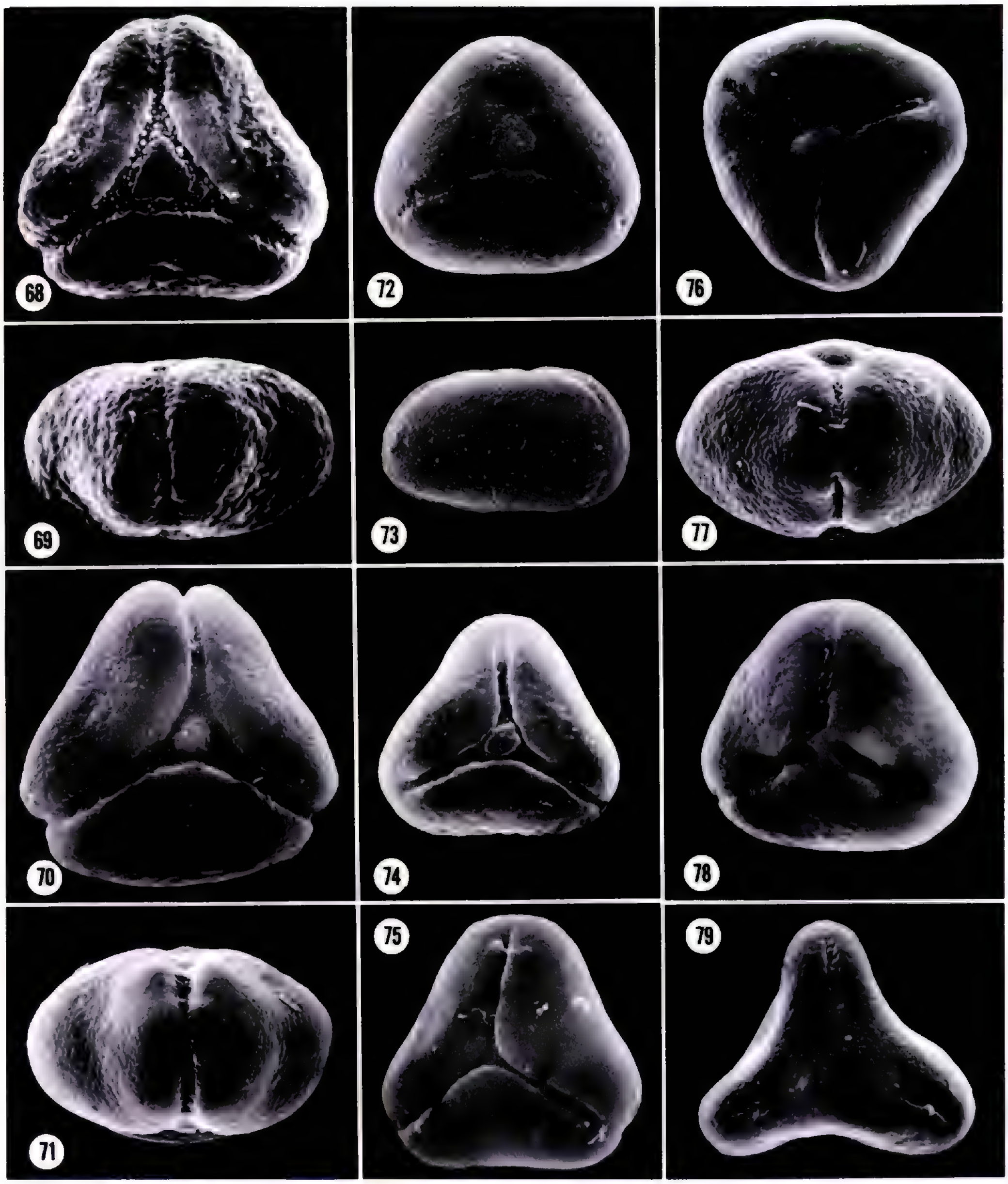
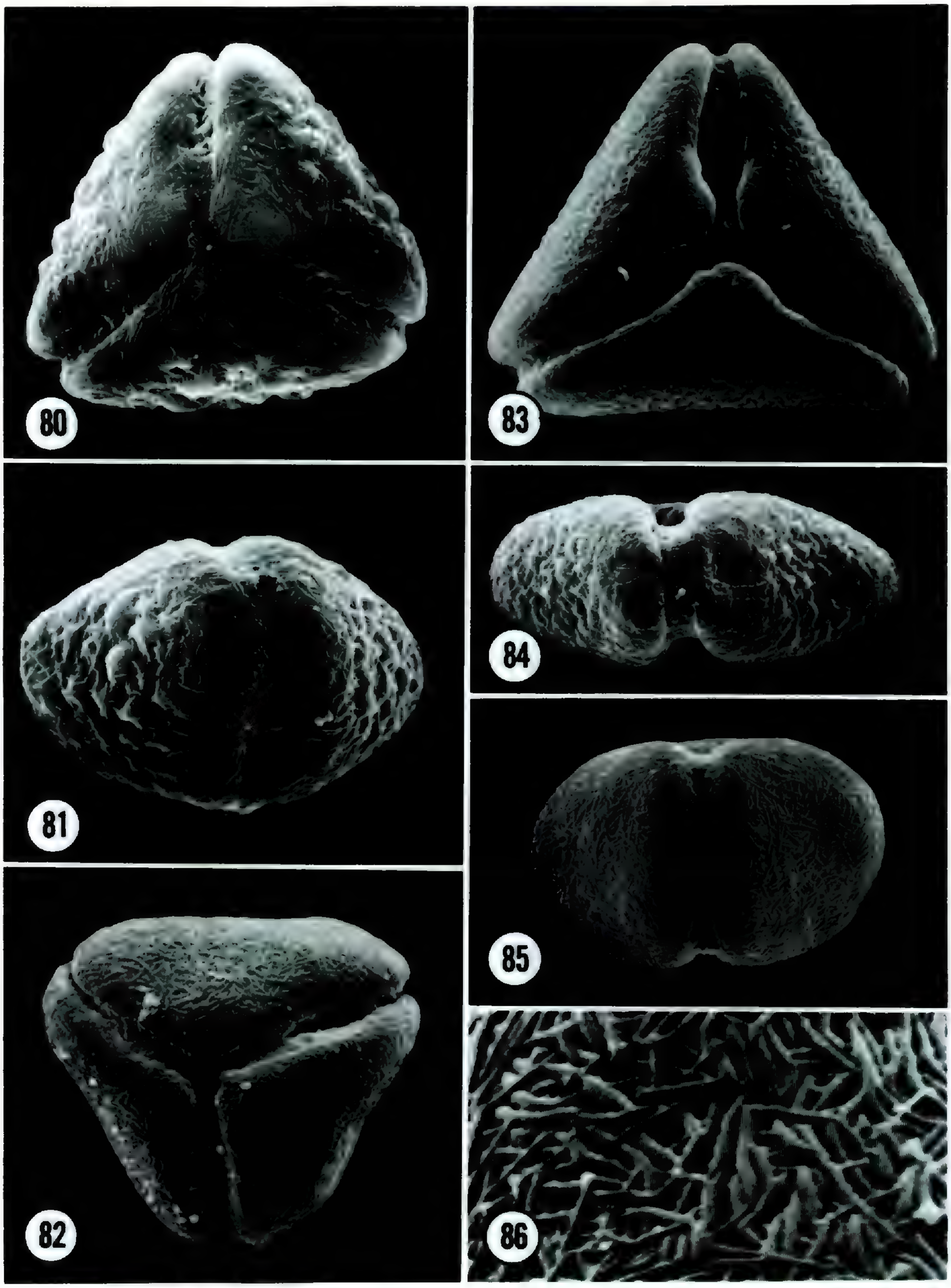
×11,000.—64. *P. rufa* var. *tentaculifera* Rizz., *Ducke 1919* (K), Brazil. Detail of equatorial exine, ×8,700.—65. *P. magdalenae* (Cham. & Schldl.) Eichler. Detail of equatorial exine, ×6,900.—66. *P. retroflexa* (Ruíz & Pavón) Kuijt, *Nee & Hanson 14038* (F), Panama. Detail of equatorial exine, ×7,200.—67. Detail of equatorial exine. Note interrupted foot layer filled with endexine (long arrow) and localized endexine along lower surface of foot layer (short arrow). Perforation (p), ×8,000. All lines in micrographs equal 1 μm.

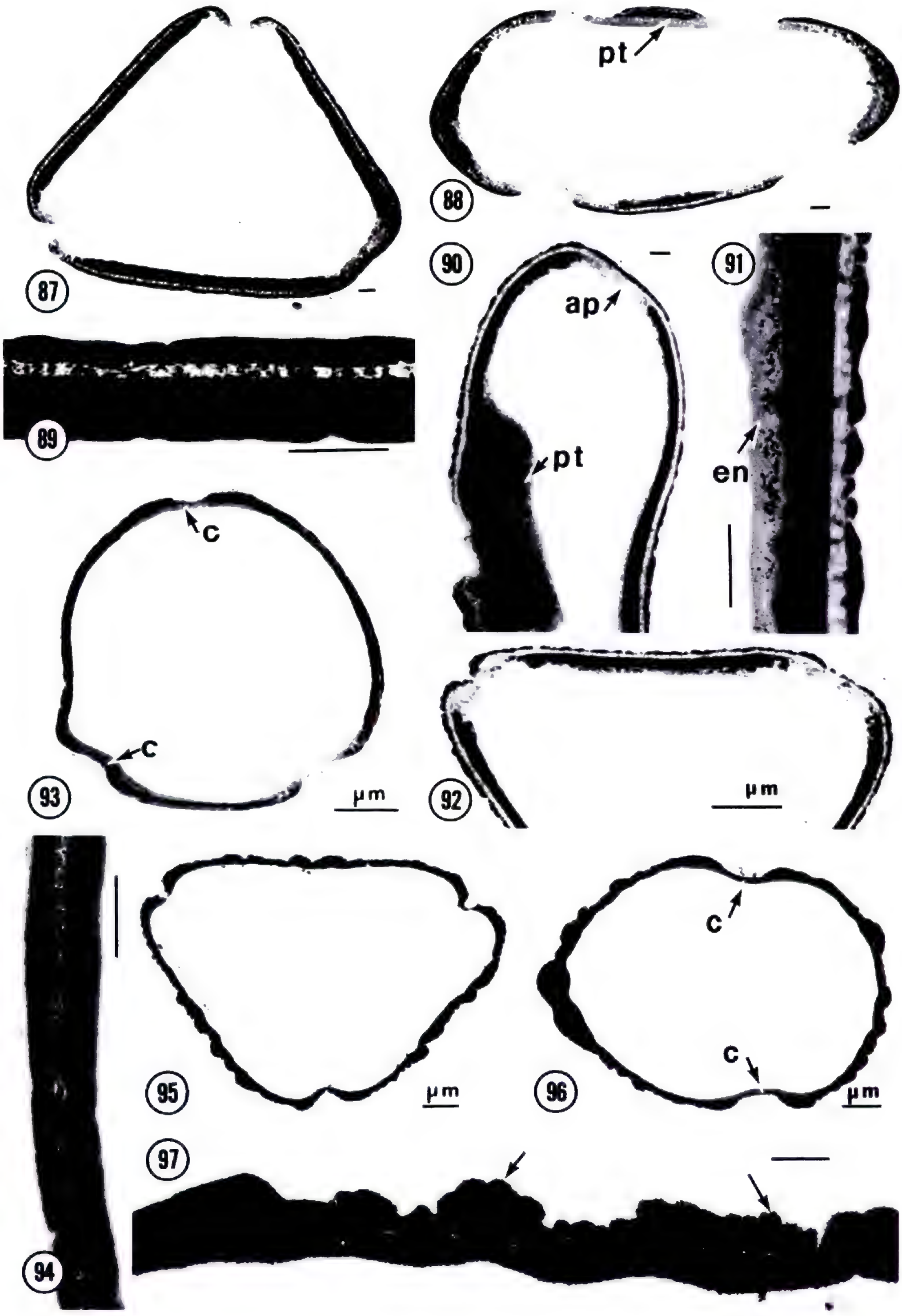


FIGURES 68–79. Comparisons between *Cladocolea* Tieghem (68, 69, 72, 73) and *Struthanthus* Martius (70, 71, 74–79) (SEM).—68. *C. glauca* Kuijt (Type III). Polar view of parasyncolpate grain with low profile striato-rugulae, ×1,120.—69. *C. glauca* Kuijt. Equatorial view, ×1,120.—70. *S. deppeanus* (Cham. & Schldl.) Blume (Type I-B2). Polar face of parasyncolporoidate heteropolar grain, ×1,400.—71. *S. deppeanus* (Cham. & Schldl.) Blume (Type I-B2). Equatorial view, ×1,400.—72. *C. microphylla* (H.B.K.) Kuijt (Type II). Polar view of diploparasyndemicolporate grain. The prominent endoapertures are not visible in the SEM, ×1,120.—73. *C. microphylla* (H.B.K.) Kuijt (Type II). Interapertural equatorial view, ×1,120.—74. *S. dichotrianthus* Eichler, *Woytkowski 8269* (UC), Peru (Type I-A2). Polar view of diploparasyndemicolporate heteropolar grain. Opposite face of this grain is diplosyndemicolporate, ×1,120.—75. *S. belizensis* Lundell (Type I-AI). Polar face with barely discernible endoapertures, ×1,400.—76. *S. marginatus* (Desr.) Blume, *Barlow 1420* (UC), Costa Rica (Type I-B2). Polar face of diploparasyndemicolporoidate heteropolar grain. Opposite face 3- or rarely 2-demi-colporoidate, ×1,120.—77. *S. marginatus* (Desr.) Blume, *Barlow 1420* (UC), Costa Rica (Type I-B2). Equatorial view showing apertures discontinuous at the equator, ×1,120.—78. *S. dichotrianthus* Eichler, *Woytkowski 8269* (UC), Peru (Type I-A2). Polar face of 3-demicolporate heteropolar grain. Opposite face syndemicolporate, ×1,120.—79. *S. panamensis* (Rizz.) Barlow & Wiens, *Davidson 431* (MO), Panama (Type II-C). Note the concave shape and poorly defined colpi near the center of the polar face, ×1,120.



FIGURES 80–86. Brazilian *Struthanthus* spp. (Type III).—80. *S. uraguensis* (Hook. f. & Arnell) G. Don, *Hatschbach 17641* (UC), Brazil. Polar view, ×1,500.—81. *S. uraguensis* (Hook. f. & Arnell) G. Don, *Hatschbach 17641* (UC), Brazil. Equatorial view, ×1,500.—82. *S. concinnus* Martius. Polar view, ×1,500.—83. *S. vulgaris* Martius. Polar view, ×1,500.—84. *S. vulgaris* Martius. Equatorial view, ×1,500.—85. *S. concinnus* Martius. Equatorial view, ×1,500.—86. *S. concinnus* Martius. Detail of equatorial sculpturing revealing striato-rugulae, ×6,000.

ened, highly perforate. Interstitium well defined, granular rarely exhibiting columellae or columellae-like structures. Foot layer continuous, with smooth upper and scalloped lower edge. Endexine continuous around grain. Polar endexine extremely thick, up to eight times thicker than equatorial ektexine, dense, filled with osmiophilic granules; equatorial endexine irregularly



FIGURES 87–97. Ultrastructural comparisons between *Cladocolea* Tieghem and *Struthanthus* Martius (TEM). 87–89. *C. harlingii* Kuijt, *Harling 6094* (S), Ecuador. 90–92. *S. panamensis* (Rizz.) Barlow & Wiens, *Davidson 431* (MO), Panama. 93, 94. *S. costaricensis* Standley. 95–97. *S. uraguensis* (Hook. f. & Arnell) G. Don, *Hatschbach 17641* (UC), Brazil.—87. Thin section through equator, ×1,200.—88. Section perpendicular to polar face through polar thickening (pt) at apocolpium and adjacent colpi, ×2,800.—89. Detail of equatorial exine revealing rarely perforate tectum, granular interstitium, and thick foot layer, ×14,000.—90. Section perpendicular to pole

thickened with small internal gaps often filled with osmiophilic granules thickest in midequatorial regions, thinning near ektexine bordering apertures; apertural endexine loosely granular.

Tectum/Equatorial interstitium//Foot layer: 1:2.

Species and specimens examined: *Struthanthus panamensis* (Rizz.) Barlow & Wiens.

TYPE III

Exomorphology: radial symmetry, isopolar. Shape: *amb* variable ranging from triangular to triangular slightly concave and convex; oblate rarely suboblate. Apertures: syncolpi, rarely parasyncolpi, colpi typically broadening and disrupted near the equator; colpal margins often thickened at the center of the polar face. Sculpturing: ranging from uniformly to nonuniformly prominent striato-rugulate sculpturing elements sometimes randomly coalescing in equatorial areas to form mounds or more elongate ridges; colpal margins psilate or more rarely exhibiting striato-rugulae. Exine usually evenly thickened at equator, but several species (e.g., *S. flexicaulis, S. vulgaris*) exhibiting thickened midequatorial exine.

Endomorphology: ektexine and endexine present. Ektexine organized into tectum, granular interstitium, and foot layer. Tectum irregularly thickened, outer surface elaborated into small excrescences representing striae in cross-section, rarely perforate. Interstitium narrow, granular, surrounded by a finely granular matrix. Foot layer thick, continuous, upper surface ranging from smooth to granular, lower edge randomly scalloped. Endexine homogeneous, absent in interapertural equatorial areas, present beneath apertures and polar faces.

Tectum/Equatorial interstitium//Foot layer: 1:2 to 2:1.

Species and specimens examined: *Struthanthus concinnus* Martius, *Irwin 2250* (UC), Brazil; *S. flexicaulis* Martius, *Irwin et al. 10771* (MO), Brazil, *Lima 7366* (UC), Brazil; *S. polyrhizus* Martius, *Bradi 16933* (GH, MO), Brazil; *S. pterygopus* Martius, *Glaziou 2599, 4821* (NY), Brazil; *S. salicifolius* Martius, *Pereira 897* (MO), Brazil; *S. syringifolius* Martius, *Krukoff 562AA* (NY), Brazil; *S. uraguensis* (Hook. f. & Arnell) G. Don, **Hatschbach 17641* (UC), Brazil, *Smith & Reitz 12449* (MO), Brazil; *S. uraguensis* var. *brevipedunculata* Chodat & Hassler, *Hassler 7531* (A), Paraguay; *S. vulgaris* Martius, **Hatschbach 16483* (UC), Brazil.

Discussion

The following sections discuss pollen characters among small-flowered neotropical Loranthaceae and their bearing on the interpretation of intra- and intergeneric relationships within the complex.

SIZE

Most small-flowered genera possess medium-sized grains which, because of their predominantly oblate shape, exhibit a significantly longer equatorial than polar axis.

The majority of largest size pollen (P: 25–30 μm; E: 32–50 μm) characterizes *Dendropemon, Oryctanthus, and Ixocactus.* At the opposite end of the range, the smallest size pollen occurs in *Maracanthus* and *Oryctina* (P: 14–20 μm; E: 23–30 μm).

Pollen size is variable among species of *Phthirusa, Cladocolea,* and *Struthanthus.* Both *Cladocolea* and *Struthanthus* exhibit clusters of species whose pollen sizes significantly differ. In *Cladocolea,* pollen of *C. harlingii* (15 μm by 25 μm), for example, is significantly smaller than that of *C. grahamii* (28 μm by 41 μm). Similarly, pollen of *Struthanthus leptostachyus* (15 μm by 30 μm) is strikingly smaller than pollen of most Brazilian *Struthanthus,* particularly that of *S. syringifolius* (33 μm by 47 μm) (cf. Figs. 13, 22).

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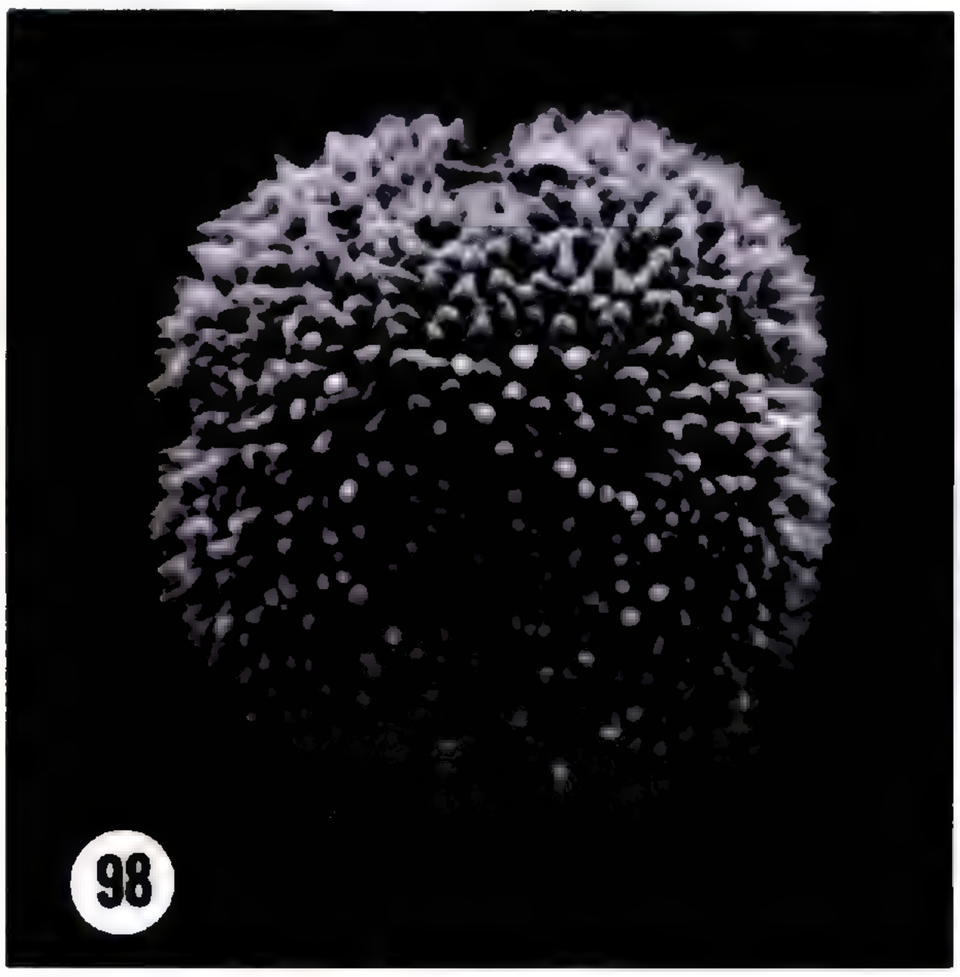
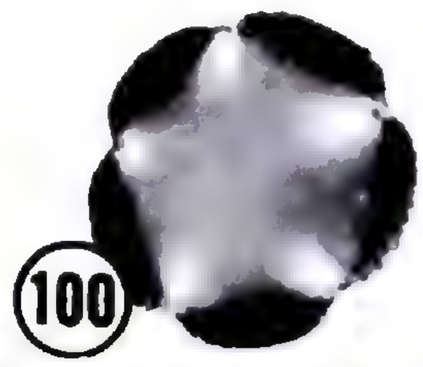
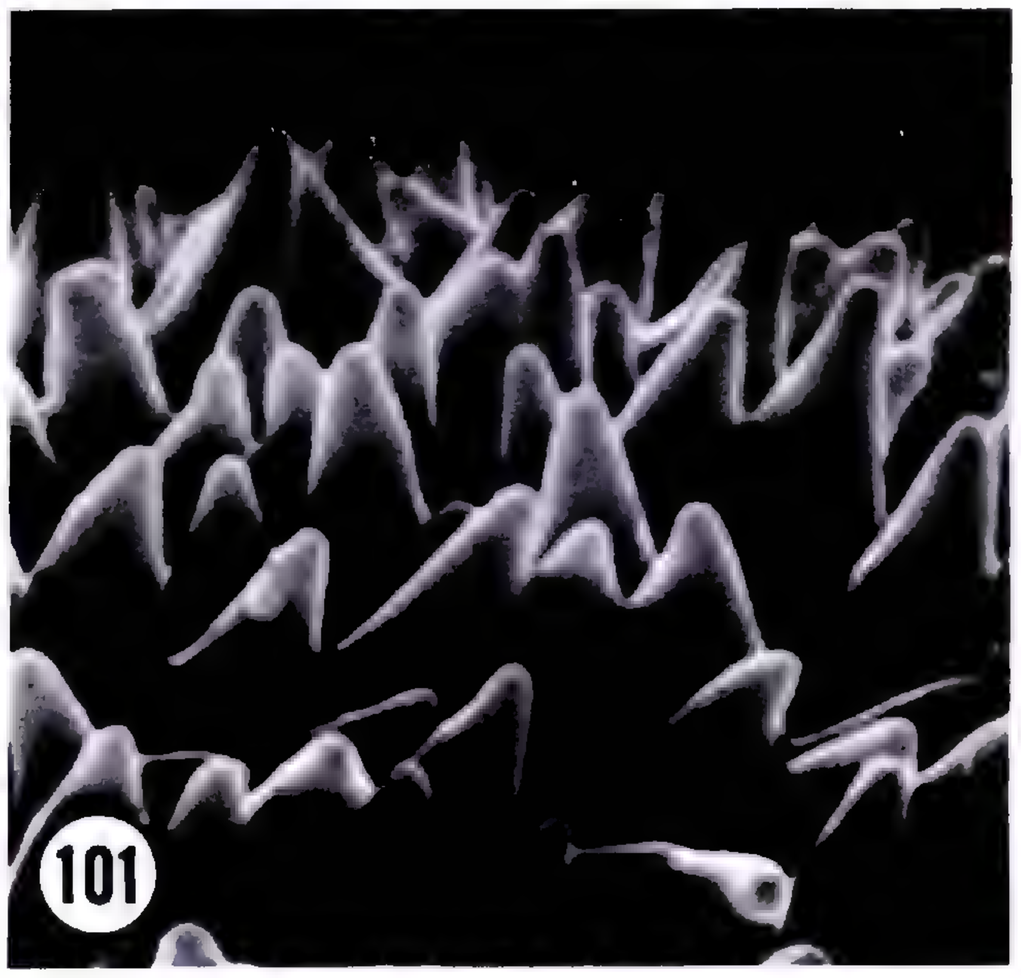
revealing prominent polar thickening (pt), granular-filled aperture (ap), and equatorial exine, ×2,500.—91. Detail of equatorial exine revealing perforate tectum, well-defined interstitium, thick foot layer, and well-developed endexine (en), ×11,500.—92. Thin section of portion of grain through equator showing granular filled apertures and interapertural equatorial endexine, ×2,000.—93. Section through equator including colpal membranes (c), ×1,500.—94. Detail of equatorial exine organized into rarely perforate tectum, poorly defined, granular interstitium, and foot layer, ×11,500.—95. Section through equator, ×1,250.—96. Section perpendicular to equator along polar axis encompassing equatorial sculpturing and colpal membranes (c), ×1,250.—97. Detail of equatorial exine organized into irregularly thickened tectum representing striae in cross-section (arrows), narrow, poorly defined interstitium and irregularly thickened undulate foot layer, ×8,500. All lines in micrographs, unless otherwise indicated, equal 1 μm. Micrographs with μm marking on photograph equal 5 μm.







FIGURES. 98–104. *Ixocactus hutchisonii* Kuijt.—98. Polar view (SEM), *Tamayo 2526* (ILL), Venezuela, ×1,950.—99. Polar view of 4-aperturate grain (LM), *Steyermark et al. 111592* (F), Venezuela, ×500.—100. Polar view of 5-aperturate grain (LM), *Steyermark et al. 111592* (F), Venezuela, ×500.—101. Detail of surface sculpturing (SEM), *Tamayo 2526* (ILL), Venezuela, ×10,500.—102. Section through exine including portion of aperture (lower right) (TEM). The point of demarcation between Types I and II exine organization is marked by the arrow, ×3,200.—103. Detail of Type I exine organization showing solid sculptural-structural elements and a solid, variably thickened foot layer separated by a narrow, granular interstitium (in) (TEM), ×8,000.—104. Detail of Type II exine organization. The ektexinous elements rest on a thin, loosely organized, discontinuous endexine (en) (TEM), ×8,000. All lines in micrographs equal 1 μm.

POLARITY

Though all small-flowered genera are typified by isopolar pollen, several species of *Phthirusa* and *Struthanthus* exhibit heteropolar pollen which may be uniformly present within a population or mixed with isopolar grains.

Heteropolar pollen features are restricted primarily to differences in aperture types between the two polar faces. The most common heteropolar aperture combination is associated with species of *Struthanthus* in which, among diploaperturate grains, one polar face is parasyndemicolpate while the opposite face is either syndemicolpate or, less frequently, 3-demicolpate (cf. Figs. 74, 78). Rarely, one set of apertures is longer than those of the opposite face (e.g., *Phthirusa angulata, Struthanthus cassythoides*).

SHAPE

Oblate pollen characterizes the small-flowered complex. Though all genera, excluding the suboblate *Ixocactus,* exhibit a mean oblate pollen shape, species of *Cladocolea, Oryctina,* and *Oryctanthus* are strictly oblate in contrast to those of *Dendropemon, Phthirusa,* and *Struthanthus* which also possess suboblate, and more rarely, oblate spheroidal grains.

Pollen *amb* is more variable than equatorial shape ranging from trilobate extremely concave among *Dendropemon* and *Phthirusa* pro parte to circular in *Oryctanthus* and *Ixocactus.* Despite this wide variation, the *amb* of most small-flowered genera is triangular to triangular slightly convex or, less frequently, concave.

APERTURES

Small-flowered genera are predominantly simple aperturate though particular species of *Cladocolea* and *Struthanthus* do, however, exhibit small, rectangular to elliptical to U-shaped slits lying perpendicular to the colpus at the periphery of the polar thickening (Figs. 7–11).

The simple apertures of small-flowered genera are predominantly diploaperturate, i.e., a set of apertures each restricted to a polar face and discontinuous at the equator usually separated by a narrow bridge of exine. Three diploaperturate types prevail: 1) diploporate-diplobrevidemicolpate; 2) diplosyndemicolpate; and 3) diploparasyndemicolpate.

The first type characterizes all *Dendropemon* and three *Phthirusa* species. Apertures in these taxa are connected by a subsurface triradiate polar thickening at each face (Figs. 25, 27, 28). The second type characterizes all remaining *Phthirusa* (excluding *P. squamulosa*) and particular species of *Cladocolea* and *Struthanthus.* The third type is restricted to a few species of *Cladocolea* and *Struthanthus.*

Though a diploaperturate condition predominates among the small-flowered genera, *Phthirusa squamulosa, Maracanthus,* and several species of *Struthanthus* and *Cladocolea* possess synaperturate grains.

The compound apertures among species of *Cladocolea* and *Struthanthus* range from poorly defined colporoidate to well-defined prominent colporate and sagittate types largely associated with diploaperturate arrangements.

The compound apertures of *Oryctanthus* are unique within the family. When viewed in the scanning electron microscope they appear as narrow, short, slightly opened slits to broad, short, open, elliptical colpi located at the tips of the raised triradiate polar thickening. Optical sections just below the pollen surface reveal, however, a sagittate endoaperture (Figs. 42–45).

The (3–)4–5 colpate apertures of *Ixocactus,* which vary within and among populations (see Table 1), are unique within the family (Figs. 99, 100).

SCULPTURING

Small-flowered genera are basically uniformly sculptured though some species do show slight sculptural differences between polar and/or colpal margins and equatorial areas.

Most taxa exhibit only slightly sculptured surfaces ranging from psilate-perforate and/or foveolate to shallowly ridged and/or striato-rugulate. All three sculpturing types occur among *Cladocolea, Phthirusa, and Struthanthus.* Among Brazilian species of *Phthirusa* and *Struthanthus,* the exine is elaborated into pronounced striato-rugulae and ridges. In *Struthanthus uraguensis, S. flexicaulis, S. vulgaris,* and *S. polyrhizus* these striato-rugulae coalesce to form small rounded mounds with striate bases and psilate apices (Figs. 80, 81, 83, 84).

The sculpturing of *Ixocactus,* composed of blunt-tipped spines and rectangular to more irregularly shaped ramifying elements, is unique in the complex.

EXINE STRUCTURE

The following section details exine characters within the complex. The unique exine features

of *Ixocactus* are reviewed separately at the end of this section.

The exine of all small-flowered genera (including *Ixocactus*) is divisible into ektexine and endexine.

Ektexine. The ektexine is basically of uniform organization throughout the grain. Only *Oryctanthus* and to a lesser degree *Dendropemon* exhibit disparate polar and equatorial ektexine structures. The equatorial ektexine is composed of tectum, interstitium, and foot layer.

The tectum is typically perforate ranging from rarely to highly perforate. Only *Oryctanthus* and a few species of *Struthanthus* exhibit an imperforate tectum throughout the grain. Usually evenly thickened, the tectum is variably thickened in *Struthanthus panamensis* (Fig. 91) and those species of *Phthirusa* and *Struthanthus* with pronounced striato-rugulate sculpturing (Figs. 95–97).

A granular or granular-columellate interstitium characterizes most genera. These columellae, ranging from narrow to broad, are typically irregularly shaped, often sporadic and clustered, and usually associated with a granular matrix (Figs. 63–65, 67, 89, 94). Strictly collumellate or columellate/baculate interstitia are rare, restricted to a few species each of *Dendropemon* (Fig. 40) and *Phthirusa* (Fig. 61). These columellae and/or baculae, though the dominant structural elements, remain generally small, thin, and/or irregularly shaped. In *Oryctanthus,* the interstitial organization is difficult to interpret. Thin sections reveal a narrow undulating osmiophilic zone traversed by extremely thin ektexinous strands (modified columellae?) (Fig. 47).

All genera, excluding *Maracanthus,* exhibit a continuous foot layer. Varying at the species level, the foot layer ranges from evenly thickened to undulate and variably thickened, the latter most pronounced in *Phthirusa platyclada* and the Brazilian species of *Struthanthus* (Figs. 41, 97). The upper surface is either smooth and clearly defined or granular and poorly defined. The lower surface can be smooth, coarsely granular, and/or broken by small gaps (Figs. 67, 89, 92).

In most genera, the foot layer ranges from as thick as or up to twice as thick as the tectum plus equatorial interstitium (1:1 to 1:2) with the reverse ratio (2:1) occurring among Brazilian *Struthanthus* where the tectum is prominently sculptured.

In most genera the polar ektexine reflects an organization similar to that in equatorial areas. The former differs in the usually thicker imperforate tectum and narrower less well-defined interstitium. *Oryctanthus,* with its strikingly different polar and equatorial ektexine organizations, is unique within the complex. Here the thick polar interstitium, filled with irregularly shaped ektexinous segments and numerous osmiophilic granules, is in sharp contrast to the equatorial interstitium represented by a narrow osmiophilic stratum traversed by thin ektexinous strands (cf. Figs. 47, 49).

Ektexine organization in lobar and peripheral equatorial areas near apertures is represented by isolated, irregularly shaped segments pendent from a solid, imperforate tectum (Figs. 36, 39, 88).

In *Ixocactus,* the organization of the upper ektexine into large, solid, irregularly shaped segments and bifurcating spines as well as the absence of an interstitium and basal ektexine in large non-apertural regions of the grain, isolate this genus from other members of the small-flowered complex.

Endexine. Endexine is typically present in apertural, lobar, and polar regions but absent in interapertural equatorial areas. In most *Struthanthus, Cladocolea, Phthirusa* species and *Maracanthus,* polar endexine is thickest at the center of the polar faces, this reaching its greatest development in *Struthanthus panamensis* (Fig. 90).

Endexine patterns in *Oryctanthus, Dendropemon,* and *Phthirusa* species with trilobate pollen differ from the majority of small-flowered genera. Polar endexine is typically absent but equatorial endexine is present though thin, irregularly thickened, and locally discontinuous. In *Oryctanthus,* endexine is also present and prominently thickened beneath the equatorial ridge (Fig. 49). The absence of polar endexine in these taxa suggests that the triradiate polar thickening visible in the light microscope is largely due then to development of ektexine rather than endexine, in contrast to those polar thickenings among *Cladocolea* and *Struthanthus* species.

The highly discontinuous granular endexine restricted to certain portions of the pollen wall in *Ixocactus* is unique within the complex.

POLLEN TRENDS

The following sections analyze pollen trends among the small-flowered genera. Pollen char-

acters of the more primitive large-flowered neotropical genera are used for out-group comparisons. Pollen features of *Ixocactus* are discussed separately at the end of these sections.

Polarity. Isopolarity is basic for the complex while heteropolarity represents the derived state. Heteropolarity, characterizing several species in the morphologically more advanced genera *Struthanthus* and *Phthirusa,* has developed independently among small-flowered loranths. The recent evolutionary occurrence of heteropolarity is suggested by its frequent occurrence alongside isopolar grains within the same population, its characterization of species rather than genera, and a consistent association with aperture anomalies.

Shape. A trilobate *amb* is primitive for the complex. Restricted to *Dendropemon* and two species of *Phthirusa,* this shape most closely approaches that typical of the large-flowered genera and Loranthaceae as a whole. The rounded convex *amb* in *Oryctina* and particular species of *Cladocolea* and *Struthanthus* is derived. The truly circular *amb,* found among a few species of *Oryctanthus,* is also a highly derived condition having arisen through modification of a rounded convex shape typical of most *Oryctanthus* species.

Oblate pollen shape is basic for the complex. The presence of suboblate and, more rarely, oblate spheroidal shapes among several advanced genera as well as the absence of such shapes among large-flowered loranths suggest their derived nature.

Apertures. A diploaperturate arrangement of simple apertures is basic for the complex. The basic type consists of colpi typically fused at the poles (syn-) but narrowly discontinuous at the equator (diplodemi-) with smooth, narrow membranes sometimes disrupted and/or broader near the equator. Both the parasyn- colpal form and the synaperturate arrangement, largely peculiar to species of *Cladocolea* and *Struthanthus,* represent derived conditions.

The status of the diploporate-diplobrevidemicolpate apertures is obscure. Their occurrence in *Dendropemon* and three *Phthirusa* species and their closer similarity to apertures of the large-flowered *Psittacanthus* [see for example *P. dilatatus, P. peronopetalus* (Feuer & Kuijt, 1979)] than to any small-flowered taxa suggest primitive, probably vestigial, character states. Though primitive, the pori-brevicolpi of the small-flowered taxa do show unique modifications: encirclement of each aperture by thickened, often slightly raised exine and interconnection of all apertures by a narrow, clearly defined triradiate subsurface polar thickening.

The compound apertures of *Oryctanthus, Cladocolea,* and *Struthanthus* are judged to be "incipient" and recently derived both because of their often ill-defined shape and the absence of a compound aperture type among Loranthaceae to date (Feuer & Kuijt, 1978, 1979, 1980, work in progress). The close palynological similarities between *Cladocolea* and *Struthanthus* suggest that their elliptical to U-shaped endoapertures may have developed independently from those of *Oryctanthus.*

Sculpturing. Though the psilate-perforate sculpturing of *Dendropemon-Phthirusa* pro parte is primitive for the complex, the basic sculpturing elements adopted by most small-flowered taxa are low profile ridges and/or rugulae and/or striato-rugulae.

Two sculpturing trends are evident within the complex. The first is the development of imperforate psilate exine. This has occurred once in the morphologically remote *Oryctanthus* and again among particular Mexican and Central American *Struthanthus* and *Cladocolea* species. A second and opposite trend, restricted to Brazilian populations of *Struthanthus,* involves the elaboration of the exine into pronounced striato-rugulae which sometimes coalesce into short mounds in equatorial areas.

Exine structure. Similar ektexine organizations in polar and equatorial areas is a derived, though widely adopted, condition among the small-flowered genera. The disparate polar/equatorial ektexine organization in *Oryctanthus* may be an independently derived character within the small-flowered complex but is common among large-flowered neotropical genera.

The basic ektexine of most small-flowered taxa is organized into a thin, perforate tectum, granular/columellate or columellate/granular interstitium and a thick, continuous foot layer typically twice as thick as the tectum plus interstitium. The imperforate tectum in *Oryctanthus* and particular species of *Struthanthus* and *Cladocolea* is a derived feature. The absence of well-developed columellae in the complex combined with the increase of purely granular interstitia among species of the morphologically advanced genera such as *Struthanthus* and *Cladocolea* suggest an overall loss of columellae. The extremely narrow

interstitial strands in *Oryctanthus* would then represent highly modified, though vestigial columellae.

Endexine patterns of most small-flowered genera are strikingly similar to those of large-flowered genera. Both groups exhibit triradiately configured, thickened, often stratified polar endexine but no interapertural equatorial endexine. The thickened polar endexine arranged in a circular configuration in particular species of *Cladocolea* and *Struthanthus* is unique to the flowered complex and represents a derived condition.

INTRAGENERIC RELATIONSHIPS

Only *Phthirusa*, *Cladocolea*, and *Struthanthus* exhibit significant specific pollen variation to permit a discussion of intrageneric relationships; of these, only *Cladocolea* has been monographed (Kuijt, 1975).

Phthirusa. Pollen characters divide the genus into two major groups: Group I composed of *P. platyclada* and *P. pyrifolia* and Group II containing all remaining species. Group I species are characterized by trilobate pollen with diploporate apertures, midequatorial and triradiate polar thickenings, and a columellate/baculate exine structure. In contrast, pollen of Group II taxa, excluding *P. squamulosa*, are diplosyndemicolpate with evenly thickened midequatorial and columellate/granular exine. *Phthirusa lepidobotrys*, with its unique diplobrevidemicolpate pollen, midequatorial and triradiately thickened polar exine but consistent triangular shape and columellate granular exine, occupies an intermediate position between the two groups.

Cladocolea. Pollen characters indicate a particularly close relationship among *C. andrieuxii*, *C. loniceroides*, and *C. microphylla*, the latter two closer to each other than either is to *C. andrieuxii*. These species exhibit the only endoapertures in the genus; the latter two additionally share a rounded convex *amb* and a triangular polar thickening along colpal margins. The naturalness of this group, as suggested by the pollen data, is corroborated by similarities in floral and inflorescence structure (Kuijt, 1975, 1981a). Other species relationships are more obscure. The unique triangular concave pollen shape and uniformly wide colpal membranes in *C. inconspicua* suggest an isolated position within the genus. However, pollen of the closely related *C. inorna* and *C. clandestina* was unavailable for study. *Cladocolea oligantha* also occupies an isolated position with its triangular pollen shape, thick exine, and sharply defined circular central polar thickening. Morphologically, this species is distinguished by dimorphic inflorescences—a feature present in only one other *Cladocolea* species.

Struthanthus. Two major groups are delimited by pollen characters: Group I containing Brazilian species populations and Group II composed of remaining non-Brazilian species populations which range from Mexico to South America. This geographic distinction refers largely to populations of species since the *Struthanthus* taxa which occur in several regions (e.g., *S. marginatus, S. orbicularis, S. rotundatus*) were not examined throughout their total range.

Pollen data suggest that the Brazilian species populations are particularly closely interrelated. Pollen is uniformly isopolar, syncolpate with pronounced striato-rugulate sculpturing. In contrast, Group II species are palynologically diverse. Both iso- and heteropolar grains occur, which can exhibit either simple or compound apertures arranged in either syn- or diploaperturate arrangements. Sculpturing ranges from typically tectate-perforate to low profile striato-rugulate to rarely psilate-imperforate. The unique occurrence of highly sculptured exines among Group I species and the restriction of heteropolar pollen, compound apertures, and psilate-imperforate features to Group II species suggest two independently evolving complexes.

Among Group II species, *S. panamensis* is distinguished by its trilobate, slightly concave pollen, thinning midequatorial exine and the presence of a well-defined interstitium and midequatorial endexine, features closer to those of *Cladocolea harlingii* than other *Struthanthus* species. The isolated position of this species, as suggested by the pollen data, is confirmed by floral and inflorescence structure. This species is distinguished from all other *Struthanthus* species by its bisexual flowers arranged in monads as opposed to unisexual triads in all other species. Such characters have led to the proposal that *S. panamensis* may represent an independent branch leading into the *Struthanthus* pool (Kuijt, 1981a).

INTERGENERIC RELATIONSHIPS

Excluding the disparate pollen characters of *Ixocactus*, the pollen data suggest two basic groupings of small-flowered genera: a first group composed of *Dendropemon, Phthirusa* pro parte, and *Oryctanthus* and a second generic cluster

containing *Phthirusa* pro parte, *Cladocolea, Struthanthus, Maracanthus,* and *Oryctina.* Such an arrangement does not, however, preclude weaker intergroup relationships.

Within Group I, *Dendropemon* is closely linked to *Phthirusa* through the species *P. pyrifolia* and *P. platyclada.* All exhibit trilobate, extremely concave pollen *amb,* diploporate apertures, and a midequatorially thickened columellate/baculate exine structure. *Phthirusa lepidobotrys,* with its diplobrevicolpate midequatorially thickened but triangular pollen links the *Dendropemon*-like *Phthirusa* species to the remaining 28 *Phthirusa* species, the pollen of which is strikingly similar to particular *Struthanthus* species.

Pollen characters support a relationship between *Oryctanthus* and *Dendropemon-Phthirusa* pro parte as suggested by floral and inflorescence structures (Kuijt, 1976a) but offer no evidence for an affinity with *Maracanthus* (Kuijt, 1976b). *Oryctanthus* pollen, though quite distinct, does possess several features common to *Dendropemon-Phthirusa* pro parte pollen: a narrow, well-defined triradiate polar thickening, small diploapertures restricted to the tips of this triradiate thickening, and an equatorial ektexine structure similar to the polar ektexine organization of *Dendropemon. Oryctanthus,* however, exhibits several uniquely derived pollen features: circular *amb,* raised polar ridges encircling polar depressions, compound apertures composed of sagittate endoapertures, and an equatorial interstitium traversed by numerous thin strands. Such unique characters suggest that *Oryctanthus* is a highly derived genus with only remote ties to the *Dendropemon-Phthirusa* pro parte complex.

Among the second generic cluster, pollen characters indicate a relationship between *Struthanthus* and *Phthirusa* on the one hand and *Struthanthus* and *Cladocolea* on the other.

Struthanthus is linked to *Phthirusa* through pollen characters of heteropolarity, oblate-spheroidal shape, apertures with protruding colpal margins, and pronounced striato-rugulate sculpturing. *Phthirusa* species remain palynologically distinct from *Struthanthus* through consistent triangular *amb* and a well-defined columellate-granular interstitium—the latter closely resembling a *Dendropemon* feature.

Pollen suggests an even closer relationship between the Mexican–Central American *Struthanthus* species and *Cladocolea,* particularly species with Types II and III pollen. The *Struthanthus-Cladocolea* species constellation similarly exhibits a triangular rounded convex *amb,* simple and compound apertures, syn- and parasyncolpi arranged in either diplo- or synaperturate arrangements, and a granular poorly defined interstitium. The parasyncolpi, the elliptical to U-shaped endoapertures, and granular interstitium are features unique to this group. The strong ties suggested by the pollen data are corroborated by gross morphology. The unique occurrence of geniculate styles among particular *Cladocolea* and Mexican *Struthanthus* evinces close interspecific relationships. Striking morphological similarities between certain intergeneric species pairs (*C. harlingii, S. orbicularis*; *C. lenticellata, S. polystachyus*; *C. pedicellata, S. deppeanus*) have been used to purport a polyphyletic origin for *Struthanthus* (Kuijt, 1981a). Since pollen of several key *Cladocolea* species was not examined and as *Struthanthus* pollen in each of the species pairs is not strikingly different from other *Struthanthus* nor closer to particular *Cladocolea* species, the data do little to support or deny polyphyletism in the genus.

The proposed affinity of *Maracanthus* and *Oryctanthus* (Kuijt, 1976a) is unsupported by the pollen data. Rather, the following pollen characters indicate an intermediate position between *Struthanthus* and *Phthirusa*: triangular to rounded convex *amb,* syncolpate apertures, perforate tectum with low profile striato-rugulae, circular polar thickening, and a well-developed columellate/granular interstitium.

Little pollen evidence exists for the suggested relationship between *Oryctina* and *Maracanthus* (Kuijt, 1981b) though these two genera are closer to each other than either is to *Oryctanthus.* In *Oryctina,* the rounded convex diploaperturate, psilate pollen with thickened apocolpial colpal margins resembles pollen of *Struthanthus* species, particularly *S. leptostachyus* and *S. palmeri.*

The pollen characters of *Ixocactus* indicate no relationship with any small-flowered genus. The intra- and interpopulational aperture variation, the irregularly spinulose sculpturing, and ektexine structure characteristic of *Ixocactus* are closer to those of the New World Eremolepidaceae and Old World genus *Viscum,* particularly the African species, than to any Loranthaceae sensu stricto.

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THE SYSTEMATICS OF THE APETALOUS FUCHSIAS OF SOUTH AMERICA, *FUCHSIA* SECT. *HEMSLEYELLA* (ONAGRACEAE)[1]

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ABSTRACT

A systematic revision of *Fuchsia* sect. *Hemsleyella,* a distinctive group of apetalous species restricted to the tropical Andes, is presented. Fourteen species are recognized, including three new species. Members of this group are protogynous and are hummingbird pollinated; they are generally rare and present little opportunity for sympatry or interspecific hybridization. The first reported chromosome counts for the section indicate that seven species are diploid and two are tetraploid; two possible hybrids were also tetraploid. Pollen grains in the section are large, with the longest axis usually over 100 μm long, and are basically 2-aperturate, although 3-aperturate grains are present in some species; there is no clear correlation between polyploidy and 3-aperturate pollen grains in this section. A series of specialization trends linked mostly to increasing seasonality is evident in the section: from species with leaves that are opposite-ternate, persistent and elliptic-ovate to ones with alternate, deciduous, cordate and long-petioled leaves; from terrestrial to epiphytic or rock-inhabiting shrubs; from non-tuberous to tuberous plants; and from short- or medium-length floral tubes to floral tubes over 10 cm long. In its assemblage of characters, sect. *Hemsleyella* is most similar to sect. *Ellobium,* from Mexico and Central America.

Within the highly distinctive Onagraceae, *Fuchsia* contains over 100 of the ca. 675 species in the family. It shows no obvious relationships to any of the other 16 genera and is unique in the family in its fleshly fruits and basically 2-aperturate pollen, being placed accordingly in its own tribe, Fuchsieae. The last generic monograph of the group was published by Munz in 1943. In recent years, an effort has been made towards a systematic reassessment of the entire genus, under the direction of Peter H. Raven; this has resulted so far in the revision of all the Mexican and Central American species of *Fuchsia* (Breedlove, 1969; Breedlove et al., 1982), as well as the large South American sect. *Fuchsia* (Berry, 1982).

Over three-quarters of the species of *Fuchsia* occur in South America. Among them, Hemsley (1876) first recognized the existence of a particular group of species characterized by the absence of petals, generally alternate leaves, and a mostly deciduous, epiphytic or saxicolous habit. This group was not formally designated, however, until Munz (1943) conferred upon it a sectional status, under the name *Hemsleyella.* Munz included 12 species and 13 different taxa in this section; one of these, *F. decidua,* is now placed in the recently described sect. *Ellobium* (Breedlove et al., 1982).

Members of sect. *Hemsleyella* are a difficult group to study because the plants are generally scarce, strongly seasonal, and occupy relatively inaccessible habitats. This section occurs sympatrically with sect. *Fuchsia* over most of its range in the tropical Andes. While conducting field studies on the latter group in 1978–1980, the author was able to observe most members of sect. *Hemsleyella* in the field and to collect series of herbarium specimens and cytological samples. In addition, loans of sect. *Hemsleyella* from numerous institutions were examined. As a result, it was possible to make a substantial revision of Munz's (1943) treatment, including new ecological, cytological, palynological, and taxonomic

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information. The following revision now recognizes 14 species in sect. *Hemsleyella,* the second largest in the genus; only six of these species are the same as ones recognized by Munz (1943), and three new species are described.

GEOGRAPHICAL DISTRIBUTION AND ECOLOGY

Distribution. *Fuchsia* sect. *Hemsleyella* is restricted to the moist slopes of the tropical Andes, from ca. 10°N to 17°S latitude. Its range coincides very closely with that of the larger sect. *Fuchsia* (see Berry, 1982, fig. 1), and therefore it is useful to discuss the distribution of the different species in light of the major structural units of the tropical Andes recognized by Berry (1982, fig. 12). Only four species of sect. *Hemsleyella* occur in the northern Andes, which includes Venezuela, Colombia, and Ecuador; two of these occupy the northern extreme of the Cordillera Oriental in Venezuela, whereas the other two occur in Ecuador. Curiously, there is no sure record of sect. *Hemsleyella* from Colombia. In the Central Andes, which include Peru and Bolivia, ten different species occur. As in sect. *Fuchsia,* a single species is found along the relatively dry Pacific slopes of the Cordillera Occidental in northern Peru; one species is restricted to the Cordillera Central in Peru, two occur in both the Cordillera Central and Cordillera Oriental, while six different species are restricted to the Cordillera Oriental in southern Peru and Bolivia.

The greatest local concentrations of species in sect. *Hemsleyella* occur in the moist valleys of Dept. Cuzco, Peru, and in the yungas of Dept. Cochabamba, Bolivia, with five species present in each area.

The most specialized species in the section occur in the Central Andes, where the most prominent tuber development, longest floral tubes, and highly seasonal species occur; unspecialized species are found in both the Northern and Central Andes.

Habitat and phenology. *Fuchsia cestroides* inhabits montane scrub vegetation in northwestern Peru and occupies the lowest altitudinal range in the section (1,100–1,700 m). All other species in the section occur in Andean cloud forest above 1,600 m, and some extend into the lower reaches of the open puna or subpáramo. *Fuchsia apetala* is most common at the upper cloud forest-puna limit and is known to reach 4,200 m in Peru, where it is subject to frequent frosts. In Venezuela, *F. membranacea* extends from 2,600 to 3,400 m at the upper limit of cloud forest and the lower reaches of open páramo.

Broad altitudinal ranges of more than 1,000 m are common in species of sect. *Hemsleyella,* by virtue of their versatile habit; plants are generally terrestrial towards their upper altitudinal limit and are often epiphytic towards the lower limit of their range.

The species of sect. *Hemsleyella* are among the most strongly seasonal in the genus. All species flower primarily in the dry season, when many are totally deciduous. This results in a limited flowering season, unlike the members of sect. *Fuchsia,* which are far less seasonal and flower over a more extended period, even though they inhabit the same areas as species of sect. *Hemsleyella.* Strong vegetative growth occurs during the rainy season, and the presence of tubers or thickened stems in species of sect. *Hemsleyella* enables food and water to be stored for the dry season flowering.

Due in part to the infrequent occurrence of plants belonging to sect. *Hemsleyella* in their native habitat, their often epiphytic or scandent habit, and their adaptation to a short dry season and extended moist season, members of this group are particularly intolerant of habitat disturbance, and the survival of many species with limited geographical ranges is being endangered by the rapid advance of forest clearing along the steep Andean slopes.

FLORAL BIOLOGY AND POLLINATION

In details of floral biology, sect. *Hemsleyella* is similar to the situation described by Berry (1982) for sect. *Fuchsia*: the flowers are strongly protogynous (Fig. 1), yet they last several days, and self-pollination can occur before stigma receptivity ends. The stigmas are generally exserted beyond the anthers, but since the flowers are pendant and the pollen contains viscin threads, pollen grains can in some cases reach the stigma of the same flower by wind or gravity. The species of sect. *Hemsleyella* are hermaphroditic, and self-incompatibility is not known for any of the species.

All species of sect. *Hemsleyella* are characterized by the presence of reddish (pink, violet, or orange), odorless, hanging flowers, all with floral tubes from 18 to 160 mm long and copious nectar production from a large nectary situated at the base of the floral tube and followed by a constriction just beyond it. With clusters of flowers

flowering simultaneously on different branches, those species offer a striking floral display, and all species are visited by hummingbirds. On legitimate visits, the hummingbirds approach the flower from below, hover while extracting the nectar from the base of the tube, and then rapidly continue on to the next flower. Few identifications of pollinators were possible, but an emerald hummingbird (*Amazilia* sp.) was seen pollinating a population of *F. tillettiana* (including *Berry 4289*) sporadically from daybreak to dusk, at 1,600 m in Edo. Mérida, Venezuela, in April 1984.

Three species of sect. *Hemsleyella, F. apetala, F. garleppiana,* and *F. inflata,* often have floral tubes over 10 cm long. The only hummingbird with a bill long enough to reach the nectar reservoir without piercing the tube is the swordbill, *Ensifera ensifera.* This remarkable hummingbird has a bill almost as long as its body, often surpassing 10 cm in length. In August 1979, swordbills were observed visiting long-tubed plants of *F. inflata,* on the outskirts of the town of Marcapata, ca. 3,000 m, Dept. Cuzco, Peru; since the flowers of this species hang down off leafless and erect or divergent shoots and often from rock overhangs, it is easy for a swordbill to approach from below and insert its bill in the tube. Because of the correspondence in bill and tube length, the bird makes contact first with its head to the stigma, then with the anthers. Individuals of *Ensifera* were also seen visiting shorter-tubed flowers of *F. chloroloba,* but their bodies did not contact the anthers.

In populations of long-tubed plants of *F. inflata* examined in August 1979, on the road from the Abra de Málaga towards Quillabamba (Prov. La Convención, Dept. Cuzco, Peru), the majority of the flowers had been pierced at the base of the floral tube by nectar robbers, as evidenced in specimens such as *Berry & Aronson 2567* and *2570.*

FIGURE 1. Portion of a flower of *Fuchsia inflata* (*Berry & Aronson 3013*) during the first day of anthesis, showing the sticky, receptive stigma and unopened anthers (protogyny).

CYTOLOGY

Fuchsia has retained the original basic chromosome number of the family Onagraceae, $n = 11$ (Raven, 1975). Unlike the situation in some of the other tribes in the family, aneuploidy and translocation systems are unknown in the Fuchsieae. Kurabayashi et al. (1962) considered the chromosomes of *Fuchsia* to be large and unspecialized for the family, with poor differentiation into heterochromatic and euchromatic portions. Polyploidy does occur in *Fuchsia* and has proven to be somewhat useful in characterizing the different sections of the genus. All species of sects. *Ellobium, Schufia, Jimenezia, Skinnera,* and *Encliandra* have been counted and were found to be diploid, except for one individual of sect. *Encliandra* (Breedlove, 1969; Breedlove et al., 1982; Raven, unpubl. data). Berry (1982) found that sect. *Fuchsia* is predominantly diploid; 37 species examined were diploid, five were tetraploid, and one species had both diploid and tetraploid populations. The monotypic sect. *Kierschlegeria* is tetraploid, and sect. *Quelusia* is entirely polyploid, with three known tetraploid and one octoploid species (Berry & Ramamoorthy, unpubl. data).

Prior to this study, no chromosome counts had been published for sect. *Hemsleyella.* Twenty-two new counts are reported here for the first time in the section, as listed in Table 1, including nine of the 14 species and two possible hybrids. The methods used were the same as those described in Berry (1982). Diploid chromosome

TABLE 1. Chromosome numbers in *Fuchsia* sect. *Hemsleyella*.

Taxon	*n*	2*n*	Collection Data
F. apetala Ruiz & Pavón		ca. 44	PERU. CUZCO: Tres Cruces, Prov. Paucartambo, *Berry et al. 2593* (MO).
	22		PERU. CUZCO: below Abra de Málaga, Cuzco-Quillabamba Road, Prov. Convención, *Berry & Aronson 3030* (MO).
		44	PERU. JUNÍN: 32 km E of Comas, on road to Satipo, *Berry & Aronson 3069* (MO).
F. aff. *apetala* Ruiz & Pavón		22	PERU. CUZCO: 91 km from Ocongate, above Marcapata, *Berry & Aronson 3014* (MO).
F. cestroides Schulze-Menz	11		PERU. CAJAMARCA: 6 km above San Benito towards Guzmango, *Berry et al. 3600* (liquid specimen, author's collection).
F. chloroloba I. M. Johnston	11		PERU. CUZCO: above Buenos Aires, Acanaco to Pilcopata, Prov. Paucartambo, *Berry et al. 2599* (MO).
	11		PERU. CUZCO: 92 km from Ocongate, above Marcapata, *Berry & Aronson 3015* (MO).
		22[a]	CULTIVATED: Berkeley, California, *Univ. California Botanical Garden accession N° 49.817*. Originally from Peru, no voucher.
F. garleppiana Kuntze & Wittmack		22[b]	BOLIVIA. COCHABAMBA: 41 m from Cochabamba on road to Chapare, *Berry 3640* (live tubers sent for cultivation to MO; same site where *Berry & Berry 2582* was collected).
F. inflata Schulze-Menz	11		PERU. CUZCO: Km 145–146 from Cuzco to Quillabamba, *Berry & Aronson 3036* (MO).
		22	PERU. CUZCO: Km 150 from Cuzco to Quillabamba, *Berry & Aronson 3040* (MO).
F. × *inflata* (probable hybrid)	ca. 22[c]		PERU. CUZCO: 88 km from Ocongate above Marcapata, *Berry & Aronson 3010* (MO).
	ca. 22[c]	44	PERU. CUZCO: 88 km from Ocongate, above Marcapata, *Berry & Aronson 3011* (MO).
F. juntasensis O. Kuntze	ca. 22		BOLIVIA. COCHABAMBA: above ENDE pumping station at Corani, *Berry 3638* (MO).
F. membranacea Hemsley	11		VENEZUELA. MÉRIDA: 13 km above Timotes, *Berry 3278* (MO, VEN).
	11		VENEZUELA. MÉRIDA: 12.5 km below Apartaderos, *Berry 3465* (MO, VEN).
F. tillettiana Munz	11		VENEZUELA. LARA: Laguna La Blanquita, Parque Nacional Yacambú, *Berry 3259* (MO, VEN).
	11		VENEZUELA. LARA: Parque Nacional Yacambú, above Sanare, *Berry 3469* (MO, VEN).
	11		VENEZUELA. MÉRIDA: 1 km above San José towards Mucutuy, *Berry 3463* (MO, VEN).
	11		VENEZUELA. TACHIRA: between Zumbador and Queniquea, *Berry 3033* (MO, VEN).
F. tunariensis O. Kuntze		22[b]	PERU. AYACUCHO: 45 km E of Tambo, towards Calicanto, *Berry 3051* (MO).

[a] Counted by Peter H. Raven.
[b] Counted by Peter Goldblatt.
[c] With bridges and fragments present at Anaphase I.

numbers were obtained for seven species and tetraploid counts for two species and two putative hybrids. Thus, as in sect. *Fuchsia,* sect. *Hemsleyella* is predominantly diploid, though apparently with a somewhat higher proportion of tetraploid species. The two tetraploid species are not closely related to each other, but each is closely related to a different diploid species. In sect. *Fuchsia,* on the other hand, most of the tetraploid species were either geographically isolated or morphologically very distinct from the rest of the species in the section.

Sympatry and Hybridization

Because of the scarcity and relatively few collections of members of sect. *Hemsleyella,* little is known about the occurrence of interspecific hybridization in this group. For some species, such as *F. cestroides, F. insignis,* and *F. pilaloensis,* there is virtually no chance for sympatry, as they occur in areas well isolated from other species in the section. Other species, such as *F. tillettiana* and *F. membranacea,* or *F. garleppiana* and *F. juntasensis,* grow in the same areas, but in different altitudinal ranges. *Fuchsia nana* and *F. apetala* generally occur close to timberline, well above cloud forest occupied by other members of sect. *Hemsleyella.*

The greatest chance for sympatry and possible interspecific hybridization is found in two areas where many members of the section have been collected: several valleys of Dept. Cuzco, Peru, and the yungas of Dept. Cochabamba, Bolivia. Nonetheless, the only observed case of close sympatry in the section was the finding of *F. inflata* and *F. chloroloba* flowering side by side in Prov. Paucartambo, Peru. Collections from plants in this area showed a series of individuals with unusual morphological variability (*Berry & Aronson 3010, 3011, 3012, 3013,* and *3016*), as well as tetraploid individuals with somewhat aberrant meiosis, providing some evidence that natural interspecific hybridization may be occurring between different members of the section there.

Members of sect. *Hemsleyella* commonly occur in the same locations as species belonging to sect. *Fuchsia.* With the marked morphological differences between those two sections, one would not expect to find intersectional hybrids. However, one possible case of intersectional hybridization has been detected in a series of Bolivian collections made by W. M. S. Brooke in August 1950, at Incachaca, Dept. Cochabamba. The sets of *Brooke 6666, 6666a,* and *6666c,* at BM, F, NY, and U, all appear to belong unequivocally to *F. juntasensis,* having been collected in different conditions of sun or shade. Sheets of *Brooke 6666b,* however, at BM, F, and NY, show some very different features. The specimen of *Brooke 6666b* at F (Herb. N° 1548145) was found "growing in the open but in high grass," according to the label; it has well-developed, opposite to terminate leaves present, whereas plants of *F. juntasensis* found growing in the sun generally flower when leafless. The shape of the flowers on this sheet correspond roughly to that expected for *F. juntasensis,* but some flowers have petals present; some of the petals are deformed and others are more or less oblanceolate and up to 15 mm long. Other flowers from the same collection lack petals altogether, and all have malformed, nonfunctional anthers. A band type nectary and connate sepal bases attest to the *Hemsleyella* par-

FIGURE 2. Habit of *Fuchsia inflata* (*Berry & Aronson 3036*) growing from tubers out of rocks and flowering on leafless stems, Prov. La Convención, Dept. Cuzco, Peru (Aug. 1978).

FIGURE 3. Epiphytic habit of *Fuchsia inflata* (*Berry & Aronson 3038*), several km below *Berry & Aronson 3036* (Fig. 2).

entage of this plant. The sheet of *Brooke 6666b* at NY is similar to that described above, only the locality is not the same: "under trees in a light forest, flowers, varying shades of mauve." The third sheet at BM bears the same label information as the NY sheet, but appears to be *F. denticulata,* which had been collected previously in the area. Most likely, *Brooke 6666b* is a series of naturally occurring hybrids between *F. juntasensis* and *F. denticulata* (sect. *Fuchsia*).

MORPHOLOGICAL CHARACTERS

Habit. All species of sect. *Hemsleyella* are perennial shrubs, lianas, or epiphytes. The presumably least advanced species in the section, such as *F. juntasensis, F. cestroides,* and *F. tillettiana,* usually occur as upright to scandent shrubs 1–3 m tall, but *F. tillettiana* has also been found as a liana with long, flexuous branches clambering through woody vegetation on steep slopes. The closely related *F. membranacea* is generally terrestrial, but requires the aid of neighboring shrubs and trees to support its branches; it is also occasionally found as an epiphyte. *Fuchsia apetala, F. inflata,* and *F. juntasensis* all occur terrestrially near their upper altitudinal limits and epiphytically at lower elevations (Figs. 2, 3). *Fuchsia pilaloensis* grows either terrestrially or epiphytically at the same elevation in western Ecuador.

The more specialized species in the section have developed adaptations to strong seasonality; they are deciduous in the dry season and possess well-developed tubers. Many of these species, such as *F. apetala, F. garleppiana, F. inflata,* and *F. chloroloba,* grow primarily among rocks and secondarily as epiphytes. *Fuchsia garleppiana* and *F. inflata* produce upright, slender stems when terrestrial and divergent to hanging branches when epiphytic (see Figs. 2, 3). *Fuchsia apetala,* on the other hand, is unique in having a prostrate, almost creeping habit, with highly congested, knotty stems when terrestrial; as an epiphyte at lower elevations, the stems are more elongate and produce slender stolons.

Leaves. Fundamental differences in leaf arrangement, shape, and persistence occur in different groups of species in sect. *Hemsleyella.* One

FIGURE 4. Extensive tuber development in *Fuchsia* aff. *inflata* (*Berry & Aronson 3010*), a shrub growing among rocks in Prov. Quispicanchis, Dept. Cuzco, Peru.

group, presumably the primitive condition in the genus and in this section, has leaves that are opposite to ternate, medium-sized (3–10 cm long by 2–5 cm wide), with short petioles (mostly 5–25 mm long), elliptic to elliptic-ovate in shape, and only slightly to moderately deciduous.

A second, more advanced group in sect. *Hemsleyella* is strongly seasonal, and the species tend to flower in the dry season when all the leaves have fallen. In some species, such as *F. insignis* and *F. nana,* the leaves are practically unknown. In cases where the leaves are known, however, such as *F. apetala, F. chloroloba,* and *F. garleppiana,* they are alternate, large (5–14 cm long by 2–7 cm wide), long-petioled (15–70 mm long) and narrowly to broadly ovate in shape, with cordate bases and typically acuminate tips. Remaining species, such as *F. pilaloensis, F. salicifolia,* and *F. tunariensis,* are intermediate between the two groups described.

Tuber development. Outside of sect. *Hemsleyella* in *Fuchsia,* the presence of tubers is known only in two species of sect. *Ellobium,* which are principally rock-inhabiting or epiphytic. Likewise in sect. *Hemsleyella,* strong tuber development occurs in the species that are most markedly epiphytic or growing among rocks. Such species as *F. apetala, F. garleppiana,* and *F. inflata* bear cylindrical tubers that often grow between rocks or even may be exposed above the soil (see Fig. 4). The tubers of *F. chloroloba* (Fig. 12) are smaller and more spherical than those of the above-mentioned species. In general, the most seasonal species of this section, with marked leaf drop during the dry season, exhibit the strongest tuber development. On the other hand, most species with opposite, basically elliptic leaves tend to grow terrestrially and preserve their leaves for most of the year. These species, such as *F. membranacea, F. tillettiana,* and *F. huanucoensis,* show very little evidence of tuber development; instead, swollen, flexuous stems sometimes occur (see Fig. 21), and appear to provide a moderate food and water storage capacity to the plant.

Floral characters. Hemsleyella is the only section of *Fuchsia* that is characterized by the absence of petals in all species. The only other

species in the genus lacking petals is *F. procumbens* (sect. *Skinnera*), although other species of sects. *Skinnera* and *Ellobium* show strong tendencies toward petal reduction.

The length and shape of floral tubes serve as reliable specific characters in sect. *Hemsleyella*. *Fuchsia cestroides* has tubes just 18–20 mm long, and *F. nana* has tubes 21–31 mm long, whereas tubes exceeding 140 mm are known in *F. apetala* and *F. garleppiana*. With the exception of *F. apetala*, relatively little variation in floral tube length occurs within species; in some of the long-tubed species, the lower range of tube lengths can be attributed to measurements of young flowers whose sepals open upon drying. In *F. apetala*, two distinct floral lengths have been found, those with tubes 10–16 cm long and those with tubes 4–8 cm long. Although only two collections with intermediate tube lengths were seen, the paucity of collections and the close similarity of stem, leaf, and pubescence characters in plants of different tube length preclude subdividing *F. apetala* into separate taxa at this time.

In sect. *Hemsleyella*, a smooth band-type nectary lines the lowermost portion of the floral tube (see Berry, 1982, fig. 48). The nectary is similar to those found in sects. *Skinnera* and *Ellobium*. It usually causes the tube to appear bulbous at the base, a condition that also results in part from the occurrence of a constriction of the floral tube just beyond the nectary. The size of the basal, bulbous part of the tube varies between species, but in all of them it serves as a kind of nectar reservoir. Hairs on the inside of the tube are generally absent in the basal part of the tube and usually appear at the constriction and further up the tube; these hairs serve to prevent the nectar from flowing down and out of the tube. Particularly large nectar reservoirs and strong floral tube constrictions are characteristic of *F. inflata* (Fig. 14) and *F. chloroloba* (Fig. 12).

The connation at the base of the sepals is characteristic of all species of sect. *Hemsleyella* and is found elsewhere in the genus only in sect. *Quelusia*. The degree of connation, as well as the shape of the sepals, largely determine how far the sepals spread or become reflexed at anthesis. Strongly reflexed sepals occur in *F. tillettiana*, *F. insignis*, *F. huanucoensis*, and *F. juntasensis* (see Fig. 21), where they are characteristically long and narrow. The sepals of most other species are moderately spreading at anthesis.

Floral color is an important character in the section, but it is usually lost upon drying. The sepals of most species differ in color from the tube, generally becoming greenish towards the apex. In *F. chloroloba*, a particularly striking contrast occurs between the glaucous, orange floral tube and the parrot green sepals. *Fuchsia inflata* also has mostly green sepals; however, their color intergrades less abruptly with that of the floral tube. Pale pink floral tubes occur in both *F. garleppiana* and *F. pilaloensis*. Other characteristic colors of floral tubes are red-purple (*F. nana*), cerise (*F. tillettiana*), and mauve or lavender (*F. juntasensis* and *F. cestroides*).

Pubescence. Vestiture characteristics, especially on the floral tubes and young vegetative parts, can be useful in distinguishing certain species of sect. *Hemsleyella*. *Fuchsia chloroloba* is remarkably glabrous throughout and is the only species with glaucous floral tubes. *Fuchsia juntasensis* and *F. membranacea* are generally subglabrous on both leaves and flowers. The flowers of *F. tillettiana* have gland-tipped hairs when fresh, a characteristic that helps distinguish it from the closely related *F. membranacea*. Several species are characterized by dense pubescence on young growth and noticeably pubescent flowers. *Fuchsia garleppiana* and *F. pilaloensis* have densely pilose or pilulose branchlets and young leaves; their floral tubes are likewise densely pilose. *Fuchsia tunariensis* is characterized by a fine, velutinous pubescence throughout, whereas *F. apetala* has a very shaggy, hirsute vestiture on young growth, ovaries, and the basal part of floral tubes.

Pollen. Pollen grains of *Fuchsia* share the distinctive features of other onagraceous pollen, such as viscin threads, protruding apertures, paracrystalline-spongy ektexine, and solid endexine. The genus is unusual, however, in its basically 2-aperturate condition, with bilaterally symmetrical grains, although a number of species have grains that are 3-aperturate and radially symmetrical. During the past ten years, *Fuchsia* has been the subject of intensive palynological studies, using light, scanning electron, and transmission electron microscopy (Nowicke et al., 1984; Praglowski et al., 1983; Skvarla et al., 1976, 1978). As a result of these studies, the most useful taxonomic characters within the genus have proven to be aperture number, viscin thread morphology, and pollen grain size.

Pollen grains of sect. *Hemsleyella* are basically 2-aperturate, but 3-aperturate grains have been found in several collections. Pollen of *Berry & Aronson 3010, 3011,* and *3012* (*F.* aff. *inflata*,

see Nowicke et al., 1984, fig. 76) is almost entirely 3-aperturate; chromosome counts of the first two collections indicate that they are tetraploid, but with meiotic abnormalities (see Cytology). In addition, pollen stainability of these collections varies widely, for example, 47%, 61%, and 99% in counts of 200 grains from different flowers of *3010* and 37%, 77%, and 88% in different flowers of *3012*. Collections of *F. inflata* from other localities have entirely 2-aperturate pollen, and two chromosome counts from these plants were both diploid, so it seems possible that the series of *Berry & Aronson 3010, 3011,* and *3012* are allotetraploid hybrids of *F. inflata* and some other member of sect. *Hemsleyella.*

In two collections of diploid species, *F. tillettiana* (*Berry 3267-B*) and *F. membranacea* (*Berry 3278*), 5–10% of the grains were 3-aperturate. A probable tetraploid collection of *F. juntasensis, Berry 3638,* has entirely 2-aperturate grains. On the other hand, grains of *Berry & Aronson 3071,* a long-tubed collection of *F. apetala,* are mostly 3-aperturate; *F. apetala* is presumably a tetraploid species. In this manner, the correlation noted by Nowicke et al. (1984) for 3-aperturate grains in *Fuchsia* to be associated with polyploidy is not clearly evident in sect. *Hemsleyella.*

The viscin threads of sect. *Hemsleyella* are all segmented-beaded, which is considered the primitive condition for the genus and is shared with sects. *Fuchsia, Quelusia, Ellobium,* and *Skinnera* (Nowicke et al., 1984). Smooth or sparsely segmented threads characterize the remaining sections.

The unusually large size of the pollen grains in sect. *Hemsleyella* is useful in distinguishing its members from other species in the genus. In seven species of sect. *Hemsleyella* examined by Praglowski et al. (1983), the longest axis measured is between 97 and 130 μm, far longer than all but two of the remaining 50 species examined.

The Evolution of *Fuchsia* sect. *Hemsleyella*

A number of unique characters or ones found only in one or two other sections of *Fuchsia* occur in sect. *Hemsleyella* and make it a very distinctive and specialized group within the genus. These specialized characters include the following, with other sections sharing them indicated in parentheses:

1) Loss of petals (one species of sect. *Skinnera,* although strong petal reduction occurs in other species of sects. *Skinnera* and *Ellobium*).
2) Smooth band nectaries (sects. *Skinnera* and *Ellobium*).
3) Presence of tubers in most species (sect. *Ellobium*).
4) Alternate leaves in some species (sects. *Skinnera* and *Kierschlegeria*).
5) Sepal connation beyond the floral tube (sect. *Quelusia*).
6) Floral tubes more than 10 cm long in some species.
7) Strong seasonality, epiphytism, and dry season flowering with accompanying leaf drop (one species in sect. *Ellobium*).

All species in sect. *Hemsleyella* lack petals, have band nectaries, and have partially connate sepals. However, not all the species possess the remaining specialized features; those species with all or most of the above traits can be assumed to be most advanced within the section, whereas the species with characters common to the majority of the other sections in the genus, such as opposite-whorled leaves, little or no tuber development, medium-length floral tubes, and little seasonality, are interpreted as indication of lower levels of specialization and the more ancestral condition of the section. Based upon these criteria, the ancestors of sect. *Hemsleyella* would have been diploid, terrestrial, non-tuberous, moderately seasonal shrubs, with opposite-ternate leaves, moderate-length floral tubes (30–50 mm long), band nectaries, and reduced petals. The present-day group corresponding most closely to this assemblage of characters is sect. *Ellobium,* which includes three species ranging from Costa Rica to Central Mexico. Although occupying a more northerly range than sect. *Hemsleyella,* sect. *Ellobium* shows specialization trends very similar to those found in sect. *Hemsleyella,* including increasing seasonality and epiphytism, reduction in petal size, and a more marked presence of tubers (Breedlove et al., 1982). On the other hand, these same trends in sect. *Ellobium* are accompanied by a progression to much more congested and defined inflorescences than those found in sect. *Hemsleyella.* Berry (1982) considers sect. *Ellobium* to be a relatively recent arrival to Central America, based on the similarities of its pollen, leaves, and flowers to the more widespread and more numerous species belonging to the South American sects. *Fuchsia* and *Hemsleyella.* Whether sect. *Ellob-*

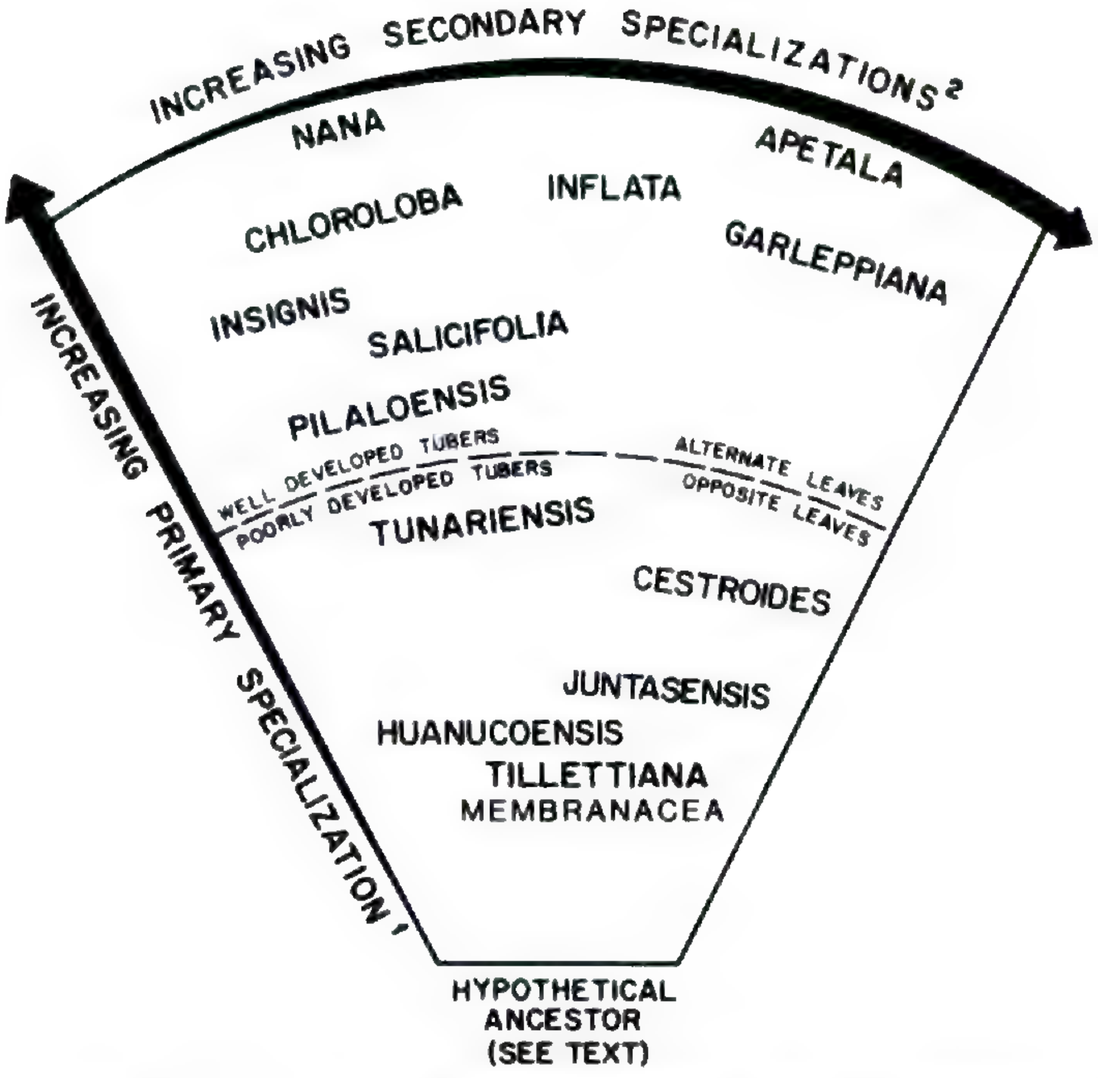

FIGURE 5. Specialization trends and interspecific relationships within *Fuchsia* sect. *Hemsleyella*.

ium is closely related to sect. *Hemsleyella* or whether their similarities are the result of convergent evolution is not presently clear. On the other hand, the altitudinal and geographical range of sect. *Hemsleyella* is very similar to that of sect. *Fuchsia*, a much larger and more generalized section of the genus; sect. *Hemsleyella* likely evolved from an early offshoot of sect. *Fuchsia* and then radiated in similar areas, occupying locally different habitats. Appropriate habitats for the epiphytic and saxicolous species of sect. *Hemsleyella* may have been more limited than the terrestrial forest edge habitat of most members of sect. *Fuchsia*, which may in part explain the greater success of the latter group, in terms of number of species and greater population sizes.

Within sect. *Hemsleyella*, individual species can be arranged schematically from least to most highly specialized, based on trends towards greater tuber development, increased epiphytism, longer floral tube length, higher altitudinal ranges, and stronger seasonality accompanied by a more deciduous habit, with large, alternate cordate leaves. A hypothetical scheme illustrating the above concepts of specialization trends and interspecific relationships within sect. *Hemsleyella* is shown in Figure 5.

HISTORY OF CULTIVATION

Because of their scarcity, non-shrubby habit, and adaptations to dry-season flowering, members of sect. *Hemsleyella* have rarely been cultivated. *Fuchsia apetala* (as *F. macrantha*) was introduced into Great Britain in 1846 (Hooker, 1846); problems associated with its cultivation were treated by van Houtte (1848).

Within the past 50 years, three different apetalous species have been cultivated at the University of California Botanical Garden at Berkeley. *Fuchsia chloroloba* (U.C. Accession N° 36.1901) flowered and was collected there in 1939. Likewise, *F. inflata* (N° 38.1052) was collected in flower at Berkeley in 1940. Finally, *F. pilaloensis* (N° 58.782-1) was collected in flower from plants in cultivation in 1961 and 1965. None of these plants or their progeny have survived until the present, however.

In a popular article on Bolivian fuchsias, Brooke (1953) stated that two tuberous species of sect. *Hemsleyella* were in cultivation in Great Britain then, but she failed to mention where, or what species were involved.

Fuchsia garleppiana, *F. apetala*, and *F. tunariensis* were briefly in cultivation at the Missouri Botanical Garden during 1979–1980, but all subsequently died.

According to Wright (1979) and Ewart (1982), there are currently no species of sect. *Hemsleyella* known to be in cultivation.

SYSTEMATIC TREATMENT

Fuchsia sect. **Hemsleyella** Munz, Proc. Calif. Acad. Sci., Ser. 4, 25: 74. 1943. TYPE: *F. apetala* Ruiz & Pavón.

Erect to scandent shrubs, prostrate subshrubs, lianas, or epiphytes. Cylindrical to subspherical tubers or thickened stems often present. Leaves opposite, ternate or alternate, usually deciduous. Flowers hermaphroditic, brightly colored, pendant, usually axillary or clustered at the branch tips, or racemose in *F. cestroides*. Sepals shorter than the floral tube and connate at the base. Petals lacking. Stamens erect, in two whorls. Pollen 2-(3-)aperturate, bilaterally or radially symmetric, with segmented-beaded viscin threads. Berry with ca. 50–250 seeds, these compressed laterally and irregularly triangular-oblong in outline. Gametic chromosome number, $n = 11, 22$.

Distribution. Cloud forest or less commonly scrub forest, puna or subpáramo in the tropical Andes from Venezuela to Bolivia (10°N to 17°S), at altitudes of 1,100–4,200 m.

Measurements used in the key and species descriptions are based on dried herbarium specimens. Leaves are often lacking when flowering specimens are collected, but leaf position can be

determined by leaf scars on the stem. Terminology for leaf venation follows Hickey (1973). The use of the term "floral tube" refers to the position of the flower from the top of the ovary to the point of insertion of the filaments or the base of the sepals.

KEY TO THE SPECIES OF *FUCHSIA* SECT. *HEMSLEYELLA*

1a. Leaves or leaf scars all or mostly opposite or ternate 2
1b. Leaves or leaf scars all or mostly alternate 7
2a. Floral tubes 18–20 mm long; pedicels 3–4 mm long ..... (2) *F. cestroides*
2b. Floral tubes 25–56 mm long; pedicels 15–75 mm long 3
3a. Floral tubes and ovaries pubescent, with pilose, velutinous or gland-tipped hairs 4
3b. Floral tubes and ovaries glabrous or subglabrous 5
4a. Floral tubes finely puberulent; sepals spreading; leaves velutinous on underside. Southern Peru and Bolivia ..... (14) *F. tunariensis*
4b. Floral tubes usually with gland-tipped hairs; sepals strongly reflexed at anthesis; leaves subglabrous. Venezuela ..... (13) *F. tillettiana*
5a. Floral tubes narrowly funnelform, ca. 7 mm wide at the mouth, 31–34 mm long; sepals narrowly lanceolate, 4–5 mm wide. Central Peru ..... (5) *F. huanucoensis*
5b. Floral tubes funnelform, 7–12 mm wide at the mouth, 25–51 mm long; sepals lanceovate, 4–11 mm wide. Venezuela, Bolivia 6
6a. Petioles 4–10 mm long; sepals divergent to recurved at anthesis, lavender-violet, same color as floral tube. Bolivia ..... (8) *F. juntasensis*
6b. Petioles 10–35 mm long; sepals spreading at anthesis, greenish; floral tube pink. Venezuela ..... (9) *F. membranacea*
7a. Floral tubes 21–31 mm long ..... (10) *F. nana*
7b. Floral tubes 32–160 mm long 8
8a. Floral tubes 70–160 mm long 9
8b. Floral tubes 32–70 mm long 11
9a. Ovary and base of floral tube glabrous or densely canescent, the tube conspicuously bulbous at the base and strongly constricted in the lower ⅓, then abruptly widened to 8–14 mm in the middle ..... (6) *F. inflata*
9b. Ovary and base of floral tube pilose to hirsute, the tube generally subcylindric, slightly bulbous at the base and 3–7 mm wide at broadest point 10
10a. Floral tubes hirsute in lower ½, rose to dull orange, usually borne on short, knotty-tortuous stems ..... (1) *F. apetala*
10b. Floral tubes pilose to subglabrous, light pink, borne on smooth or more or less elongate stems ..... (4) *F. garleppiana*
11a. Floral tubes and ovaries completely glabrous; sepals bright green throughout ..... (3) *F. chloroloba*
11b. Floral tubes and ovaries lightly pubescent to densely hirsute; sepals not entirely bright green 12
12a. Sepals 25–37 mm long 13
12b. Sepals 10–25 mm long 14
13a. The longer stamens 30–40 mm long; sepals strongly recurved at anthesis ..... (7) *F. insignis*
13b. The longer stamens 15–22 mm long; sepals spreading to divergent at anthesis ..... (12) *F. salicifolia*
14a. Floral tubes and ovaries densely pilose or hirsute 15
14b. Floral tubes and ovaries puberulent or subglabrous 16
15a. Flowers generally borne on short, knotty stems with densely packed leaf scars; floral tubes rose to orange-red. Peru and Bolivia ..... (1) *F. apetala*
15b. Flowers borne on loose shoots, not on short, knotty stems; floral tubes light pink. Western Ecuador ..... (11) *F. pilaloensis*
16a. Floral tubes and undersides of leaves densely puberulent or velutinous; leaves ovate or elliptic-ovate with subacuminate tips ..... (14) *F. tunariensis*
16b. Floral tubes and leaves subglabrous to sparsely pubescent; leaves narrowly lanceolate, with long acuminate tips ..... (12) *F. salicifolia*

1. Fuchsia apetala Ruiz & Pavón, Fl. Peruv. 3: 89, pl. 322, fig. b. 1802. Macbride, Field Mus. Nat. Hist., Bot. Ser. 13: 546. 1941. TYPE: Peru. Dept. Junín: Huasahuasi (75°31–37′W, 11°15′S), Apr. 1779, *Ruiz & Pavón* (lectotype, MA, here designated; photograph, MO). There are four Ruiz and Pavón collections at MA which are labelled as *Fuchsia apetala*; the lectotype is one of two with "N° 11/90" written on a separate label at the base of the sheet, which also contains a lengthy, handwritten description of the plant, presumably by the collectors (see Fig. 6). The label cites at the end, "Habitat Huasahuasi in elevatis humidis et frigidis. Floret abri." Figures 6–9.

Fuchsia macrantha Hooker, Bot. Mag. 72: t. 4233. 1846. Munz, Proc. Calif. Acad. Sci., Ser. 4, 25: 83. 1943, pro parte. TYPE: Peru. Dept. Junín: on trees in high mountains of Andamarca, 1836–1837, *Mathews 1197* (holotype, K-Hooker Herbarium; isotypes, K-Bentham Herbarium, OXF, P, TCD, W).

Fuchsia hirsuta Hemsley, J. Bot. 14: 69. 1876. Munz, Proc. Calif. Acad. Sci., Ser. 4, 25: 81, pl. 13, fig. 70. 1943. TYPE: Peru. Dept. unknown, June 1854, *Lechler 1989* (holotype, K).

Fuchsia unduavensis Munz, Proc. Calif. Acad. Sci., Ser. 4, 25: 81, pl. 13, fig. 71. 1943. TYPE: Bolivia. Dept. La Paz, Nor Yungas, Unduavi, 3,600 m, 13 Feb. 1907, *Buchtien 2925* (holotype, US-1177335, photographs, NY, UC; isotypes, NY, Z).

FIGURE 6. Photograph of the lectotype of *Fuchsia apetala, Ruiz & Pavón,* 1779 (MA).

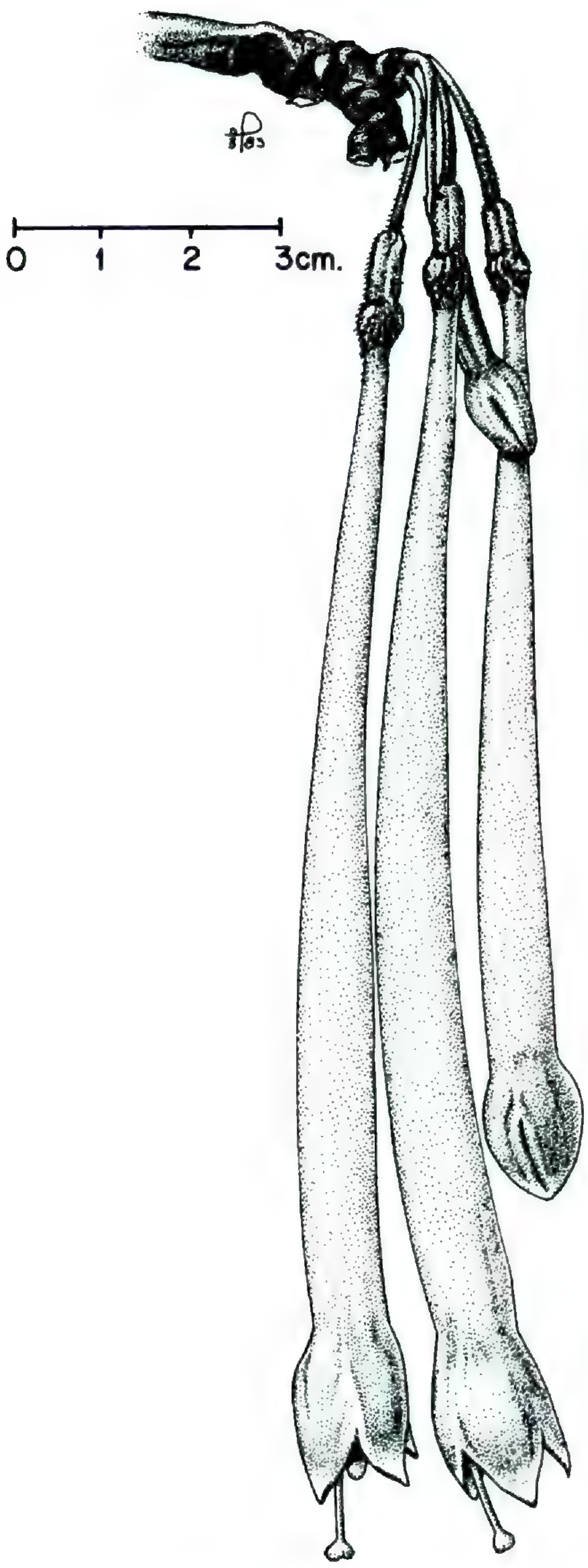

FIGURE 7. Flowering branch of *Fuchsia apetala*, long-tubed form, from *Berry & Berry 3070*, Dept. Junín, Peru.

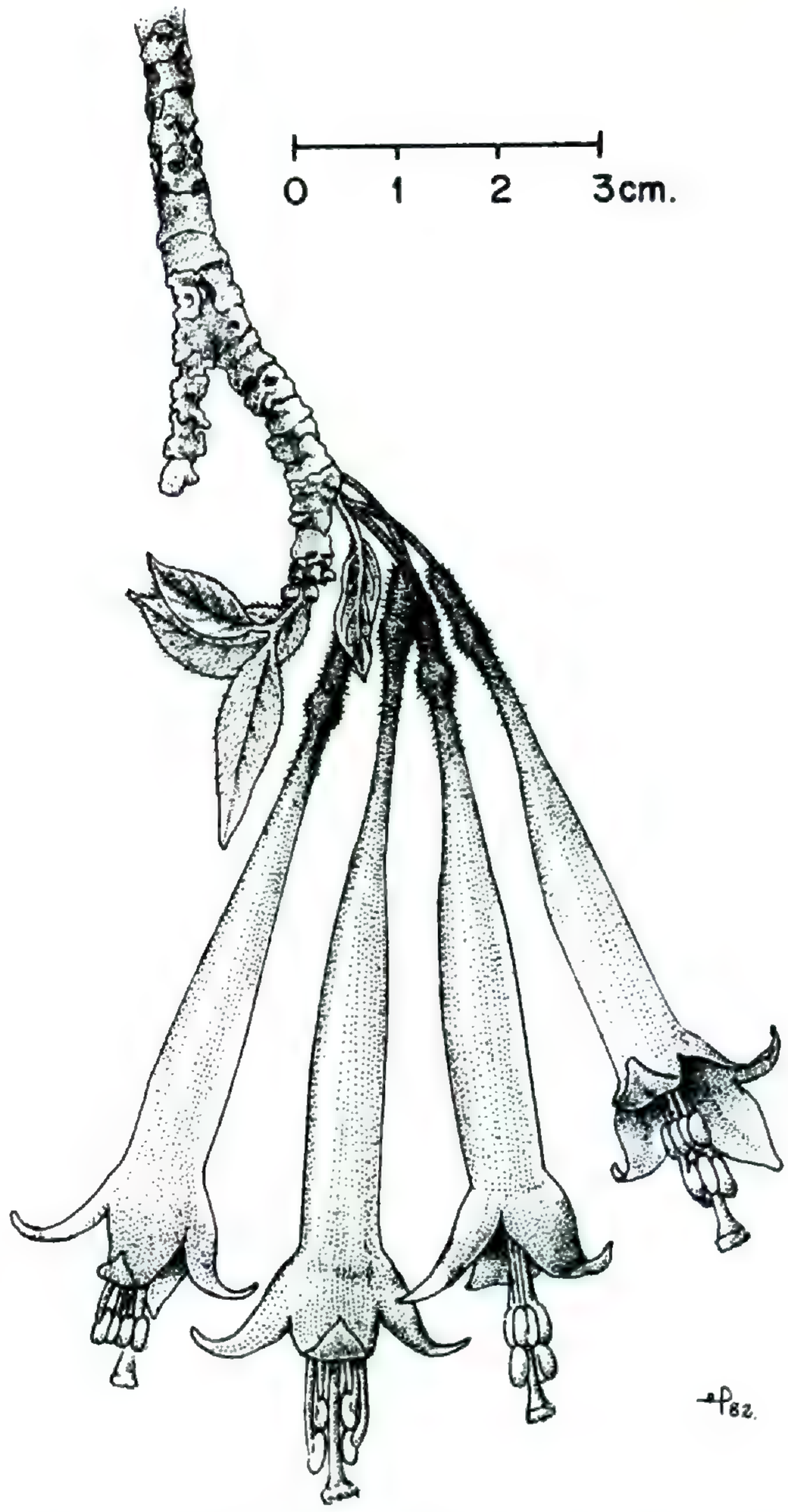

FIGURE 8. Flowering branch of short-tubed form of *Fuchsia apetala*, from *Berry & Berry 2565*, Prov. La Convención, Dept. Cuzco, Peru. Note the hirsute pubescence at the base of the floral tubes.

Prostrate to hanging subshrubs in rock crevices or on the edge of banks rich in *Sphagnum* or humus, or vine-like epiphytes on moist tree trunks. Tubers ellipsoid to cylindrical, 2–8 cm long and 1–5 cm thick, covered by copper-tan, flaking bark, often interconnected by slender stems. Stoloniferous shoots 2–12 dm long when epiphytic (lacking when terrestrial), 2–4 mm thick with freely exfoliating red-copper bark; leaves and flowers borne on short, lateral, knotty-tortuous stems with tightly packed leaf and pedicel scars, these stems rarely more than 4 cm long, 3–8 mm thick, dull gray, pilose to hirsute. Leaves alternate and usually tightly clustered at the branch tips, mostly deciduous at anthesis or present on plants flowering in shady habitats, soft membranous, subcordate to ovate-elliptic, 60–120(–150) mm long, 35–65 mm wide, apex acute to acuminate, base rounded to obtuse or subcordate, densely pilose-hirsute when young, green and subglabrous to strigose above at maturity, slightly paler and pilose below, with appressed, densely villous hairs along veins; margin sub-

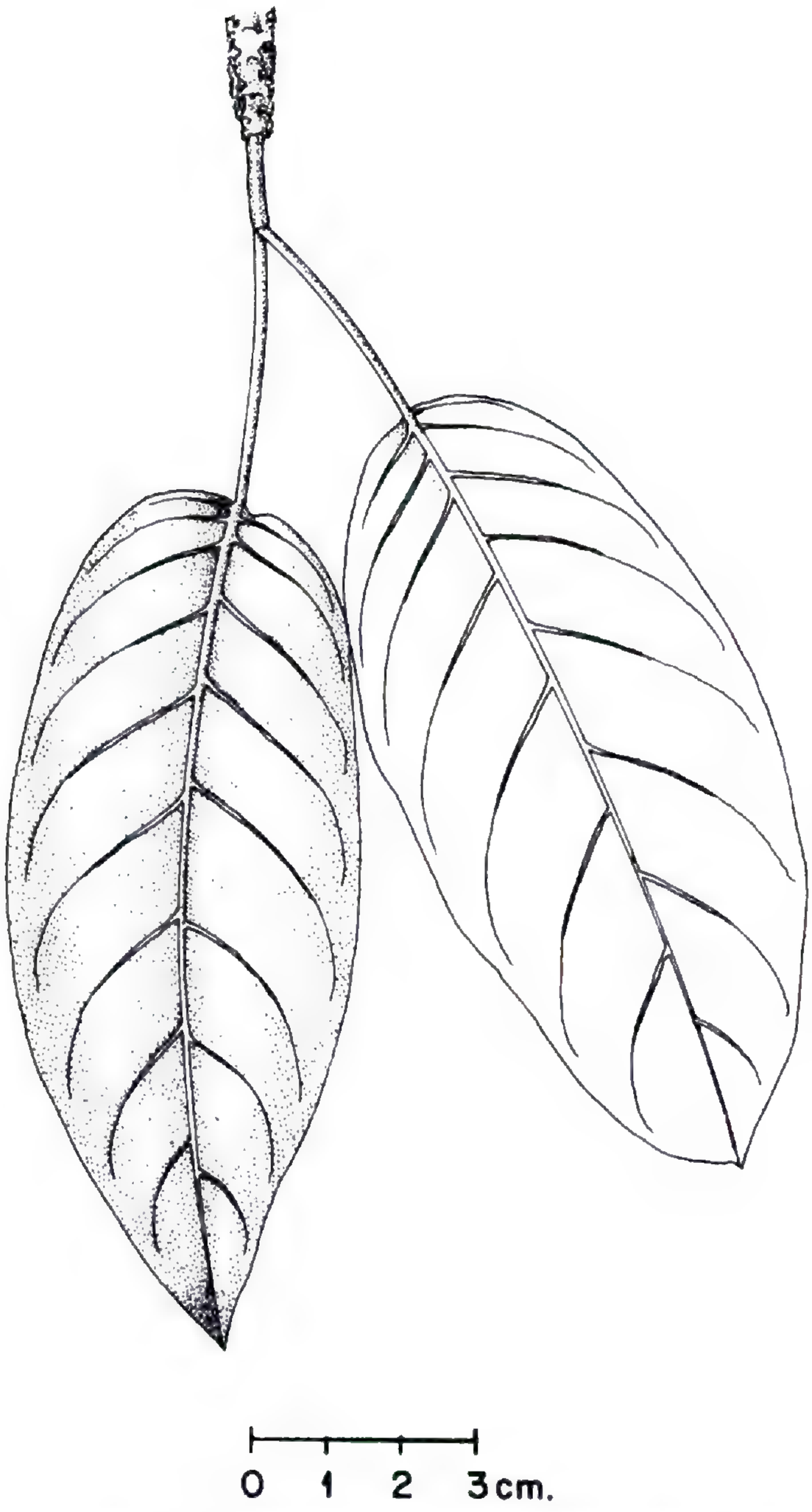

FIGURE 9. Leaves of *Fuchsia apetala*, from *Berry & Berry 2564*, Prov. La Convención, Dept. Cuzco, Peru.

entire to denticulate, secondary veins 6–8 on either side of the midvein. Petiole 25–50(–70) mm long, 2–3.5 mm thick, reddish, pilose; stipules filiform, 2–3 mm long, deciduous. Flowers crowded near the tip of lateral, knotty twigs, usually 3–12 per shoot; pedicels pilose to hirsute, (10–)18–35 mm long; ovary cylindrical, subtetragonous, 6–12 mm long, 2–4 mm thick, short pilose to densely hirsute, the hairs often shaggy and to 2 mm long. Floral tube subcylindrical, 4–16 cm long, 3–6 mm wide and somewhat nodose at the base around the nectary, then narrowed to 2–4 mm wide followed by a gradual widening until 7–10 mm wide at the rim, sometimes dilated to 8–13 mm wide just below rim, pilose to densely hirsute in the basal 1–2 cm, loosely pilose for the rest of length, inside subglabrous to villous 10–35 mm above the base. Sepals ovate, broadly acute, 16–25(–30) mm long, 7–12(–16) mm wide, usually broader than the tube, connate at the base for ⅓–½ the total length, free segments spreading to slightly recurved at anthesis. Tube rose to light orange-red, at times with a dark purple, nitid ring at the rim, sepals rose red and usually dull yellow-green distally. Nectary lustrous green-purple, lining the basal 5–6 mm of the tube. Filaments green to dull pink with age, the antesepalous ones 10–18 mm long, the antepetalous ones 8–15 mm long; anthers narrowly oblong, 3.5–4.5 mm long, 1.5–2 mm wide, yellow. Style pale green, subglabrous to densely (retrorse) villous between 10–40 mm above the base, the basal 10–15 mm usually glabrous; stigma green, globose-capitate, slightly 4-cleft, 2–4 mm long, 1.5–2.5 mm wide, exserted 1–15 mm beyond the anthers. Berry oblong, red, subtetragonous, 17–25 mm long, 8–12 mm thick, subglabrous to densely hirsute, more or less verrucose, many-seeded. Gametic chromosome number, $n = 22$.

Distribution. Eastern slopes of the Peruvian Andes from Dept. San Martín south to Dept. Puno and in Bolivia, Depts. La Paz and Cochabamba; in upper cloud forest and the lower reaches of the puna, on rocks, tree trunks and *Sphagnum* banks, (2,800–)3,200–3,850(–4,200) m, but most common around 3,600 m. Flowering principally in the dry season, from June to September. Figure 10.

Specimens examined. PERU. SAN MARTÍN: valley of Rio Apisoncho, 30 km above Jucusbamba, 7°55′S, 77°10′W, *Hamilton & Holligan 1003* (K), *1073* (K, UC). HUÁNUCO: Carpish summit, *Ferreyra 2395* (USM), *10030* (USM); about Muña and Pillao, *Lobb s.n.* (W); Yanano, *Macbride 3740* (F); Tambo de Vaca, *Macbride 4970* (F, GH). PASCO: Pozuzo, *Pearce 113* (K). JUNÍN: Prov. Concepción, 22 km E of Comas, Concepción-Satipo, *Berry & Aronson 3068* (MO, USM); 32 km E of Comas, road to Satipo, *Berry & Aronson 3069* (MO); 72 km E of Comas, *Berry & Aronson 3070* (MO, USM); 82 km E of Comas, *Berry & Aronson 3071* (MO); San José, road to Andamarca, *Raimondi 45* (USM); Prov. Jauja, Hda. Runatullo, *Weberbauer*, 1920 (MO, USM). AYACUCHO: Prov. La Mar, E massif of Cordillera Central, between Tambo, San Miguel and Hda. Luisiana, ca. 75°33′W, 12°45′S, *Dudley 11995A* (NA), *Dudley & Terborgh 12070H* (NA); Prov. Huanta, entrance to mountains of Huantas, *Raimondi 234* (USM); Prov. Cangallo, descent to Ocros, *Vargas 15891* (CUZ); Punaccuanca Pass, *West 3669* (GH, MO, UC). CUZCO: Prov. Convención, Km 140–144 from Cuzco to Quillabamba, below Abra de Málaga, *Berry & Berry 2562* (MO), *2563* (MO), *2564* (MO), *2565* (MO), *2566* (MO), *Berry & Aronson 3030* (MO, USM), *3033* (MO,

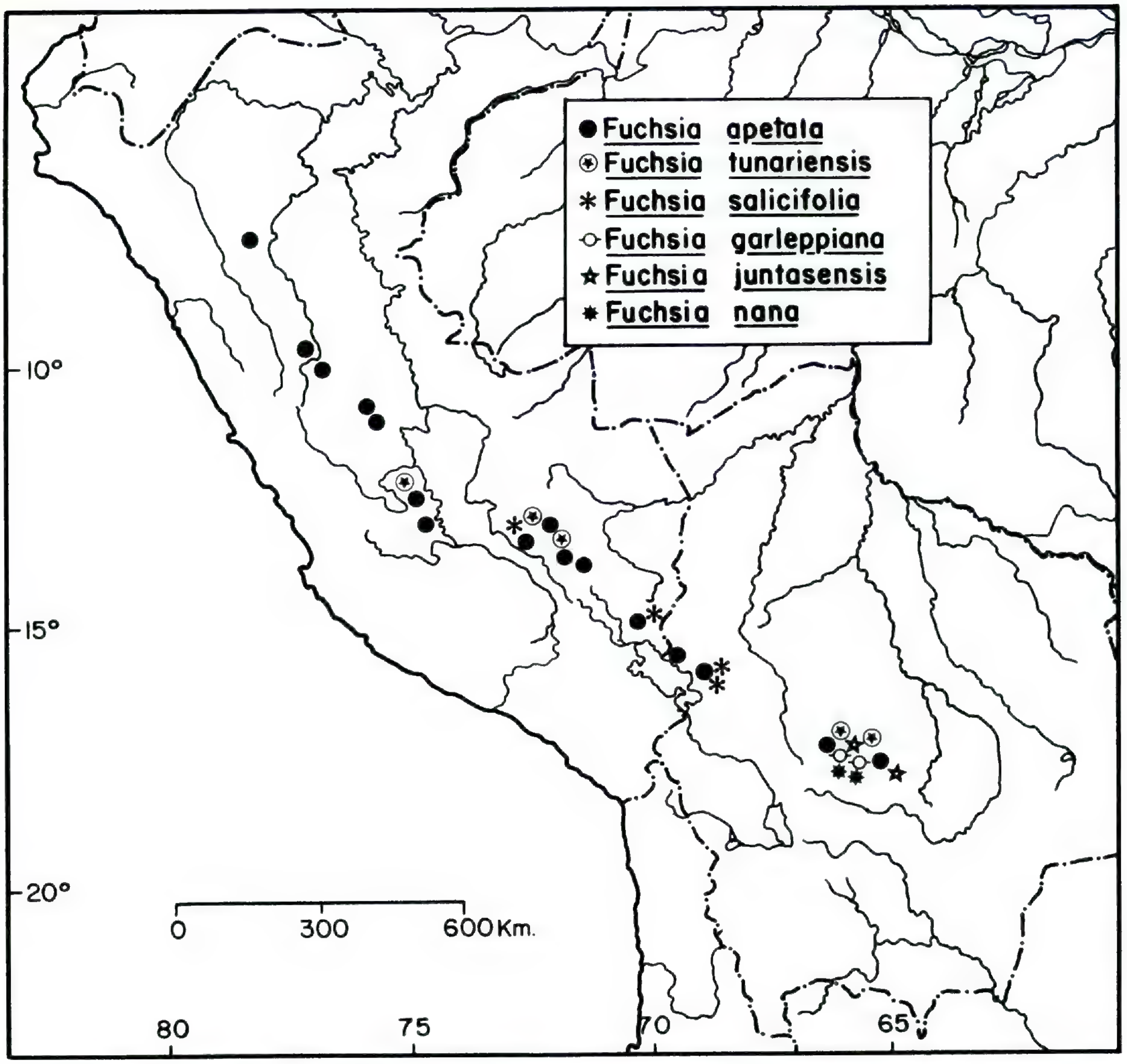

FIGURE 10. Distribution of the species of *Fuchsia* sect. *Hemsleyella* restricted to Bolivia or occurring in both Peru and Bolivia.

USM); Prov. Paucartambo, 1 km from Tres Cruces, road to Acanaco, *Berry et al. 2593* (MO—2 sheets); Piñasniog, Panticalla Pass, *Cook & Gilbert 1857* (US); Prov. La Convención, ca. 25 km NE of Hda. Luisiana and Rio Apurimac, *Dudley 11215B* (NA—2 sheets); Tres Cruces, *Gentry et al. 23435* (MO), *Pennell 13897a* (PH), *Vargas 12207* (CUZ), *Weberbauer 6975* (F—2 sheets, GH); Salcantay, *Heim,* 1848 (Z), *Rauh P1473* (RSA); Colinas de Sacsayhuamán, *Herrera 2189* (BH, F), *Vargas 1209* (CUZ); Yucay, *Soukup 715* (BH, F, USM); Prov. Urubamba, Machu Picchu, 3 km from Inca Trail in Tres Piedras Blancas at Huayruro, *Peyton & Tilney-Peyton 1056* (MO); Prov. Paucartambo, Pucara, Marcachea, *Vargas 1599* (CUZ); Prov. Urubamba, Chincheros, *Vargas 1641* (CAS, CUZ, UC), *9602* (BH, G-DEL, GH, K, MO, NA, UC); Combapata, Canchis, *Vargas 1900* (CUZ, GH); Prov. Quispicanchis, Pucuta, Chutacuchu, Marcapata, *Vargas 3750* (CUZ); Panticalla-Yanamanche, *Vargas 4432* (CUZ); Prov. Quispicanchis, Layampampa, *Vargas 6649* (CUZ); Prov. Anta, Mollepata, toward Ramicruz, *Vargas 8343* (CUZ); Prov. Calca, near Lares, *Vargas 10962* (CUZ); Prov. Paucartambo, Dtto. Marcachea, forest of Pucara, *Vargas 11170* (F, G-DEL, K, NA, UC); Prov. Urubamba, Peñas, *Vargas 15730* (CUZ); without locality, *Weddell 4771* (P); Prov. Paucartambo, between Acanacu Pass and Pillahuata, *West 7074* (GH, UC). PUNO: Prov. Sandía, 7–15 km S of Limbani, *Metcalf 30467* (A, G-DEL, MO, UC); region of Puno, *Soukup 525* (F); Prov. Carabaya, between Ayapata and Kanelluyoc, *Vargas 10789* (CUZ); Prov. Sandía, road to Oconeque, *Vargas 14852* (CUZ); Agualani to Oconeque, *Vargas 20654* (CUZ); Prov. Carabaya, *Weddell 4682* (P). WITHOUT DEPARTMENT: Churupullana, *Dombey s.n.* (F, P), *Gay s.n.* (P), *Martinet s.n.* (P). BOLIVIA. LA PAZ: Prov. Murillo, valley of Zongo, 22 km beyond summit, *Beck 2140* (LPB); Prov. Camacho, 2 km S of Ambana, *Beck 4168* (MO); Nor Yungas, 2 km from Unduavi to

Coroico, *Berry & Berry 2576* (MO); Yerbani, *Braun 38* (US); Gran Poder, 40 km N of Sorata, below Tacacoma, *Brooke 6434* (BM, F, G-DEL, NY, U); junction of road from La Paz to Coroico-Chulumani, *Brooke 6904* (BM); Unduavi, *Buchtien,* 1910 (F); Ingenio, between Sorata and Mapiri, *Cárdenas 1142* (NY), *Williams 882* (BM, K, NY); above Pongo, *D'Arcy & Bejarano 13940* (MO); Prov. Larecaja, near Sorata, *Mandon 625* (BM, F, G, G-BOIS, GH, K, NY, P, S, W); Pelechuco, *Pearce,* 1864 (BM); Murillo, 22.5 km below Zongo dam, *Solomon 8419* (MO); Sud Yungas, 16.2 km E of pass between Mururata and Illimani, *Solomon 11377* (MO); Pongo, *Tate 188* (NY—2 sheets); Cordillera Real, Rio Aceramarca, *Tate 718* (NY); Prov. Larecaja, Valley of Tipuani, *Weddell,* 1851 (P). COCHABAMBA: Km 15 of Rodeo-Mizque road, *Badcock 830* (K); Choro, Aparcita, *Brooke 6098* (BM, F, G-DEL, NY, U); Choro, 100 mi. NW of Cochabamba, above Río Cocopata, *Brooke 6134a* (BM, F, NY, U), *6243* (BM); Incachaca, *Brooke 6738* (NY), *6797* (BM); Incachaca Pass, *Brooke 6920* (U); Luruni, hot springs above Quillacollo, trail to Cochabamba, *Brooke 6786* (BM); Ayopaya, Sailapata, *Cárdenas 3369* (US); Toralapa, way to Yungas da Vandiola, *Cárdenas 3754* (POM); San Miguel, way to Morochata, Tunari, *Cárdenas 4084* (RSA); Sehuenka-Carrasco, *Cárdenas 6135* (US); Prov. Ayopaya, *Weddell 4129* (P, US). WITHOUT DEPARTMENT: *Bang 146* (BM), *2834* (F, GH, K, LE, MICH, MO, NY), *Bridges s.n.* (BM), *Pearce 771* (K).

Fuchsia apetala was the first apetalous species described in the genus, but the notable differences between Ruiz and Pavón's type description and the accompanying illustration, as well as the apparent wide variation in floral tube lengths in the species, have led to differing interpretations as to what plants should be included under this name. It is clear from the original description and from most of Ruiz and Pavón's collections labelled by them as *F. apetala,* that they applied this name to plants with pilose floral tubes 10–14 cm long, with relatively small sepals and with flowers borne on short, knotty stems (see Figs. 6, 7). The plate that accompanies the type description, however, shows a plant with much shorter floral tubes, long-spreading sepals and smooth flowering and leaf-bearing stems; these discrepancies appear to be the result of a confusion of different apetalous specimens that they collected in central Peru, and not to different forms of the same species.

The herbarium at MA contains four different Ruiz and Pavón collections labelled as *F. apetala.* One of these bears a slip of paper with the name "Cavanilles" above the label and includes a plant with ampliate, short-tubed flowers 55–60 mm long and a single, large, ovate leaf 15 cm long by 9 cm wide, but with the typical knotty stem of *F. apetala.* The remaining sheets all have long, narrow-tubed, subcylindrical flowers on verrucose stems, agreeing closely with the type description. The sheet chosen as the lectotype (Fig. 6) also contains a lengthy handwritten description very similar to the one used to describe the species and cites as the collecting locality one of the two sites mentioned in the type description, which states, "Habitat copiose in Huassahuassi et Muña nemoribus" (Ruiz & Pavón, 1802: 89). Unless there is a Huasahuasi in Dept. Huánuco, these localities correspond to two different areas, the first in Dept. Junín and the second on the Dept. Huánuco-Pasco border. Additional Ruiz and Pavón collections labelled as *F. apetala* are found at BM (three sheets, two with long floral tubes and one with a mixture of a long-tubed and a short-tubed plant), F (two fragments taken from MA, one from a long and narrow-tubed plant, the other from a short, broad-tubed individual), G (three sheets, all long-tubed, in G-DEL, G-BOIS, and G-"*Pavón 213*"), MO ("ex BM," long-tubed), and P ("*Herb. Pavón 36,*" long-tubed). Subsequent authors treating the apetalous fuchsias based their concept of *F. apetala* either on the type description (Macbride, 1941) or else on the illustration (Hemsley, 1876; Munz, 1943, 1974).

As defined here, *F. apetala* is best characterized by the presence of short, knotty or verrucose stems on which the leaves or flowers are tightly grouped, as well as by a typically pilose to hirsute pubescence on the leaves and flowers. The leaves, although generally absent when the plant flowers, are larger and more ovate-cordate than any other apetalous species (except possibly *F. insignis*), and the tubers are particularly well developed. Populations of *F. apetala* may differ considerably in floral tube length, the only species in the section to do so; nonetheless, almost all of the plants share the aforementioned traits, as well as similarly short, ovate and dull-colored sepals with rose scarlet to dull orange floral tubes.

In general, the specimens of *F. apetala* can be divided into long-tubed (10–16 cm) or short-tubed (4–8 cm) groups. The long-tubed plants, including the type of *F. macrantha,* seem to grow mostly as epiphytes in cloud forest and are restricted to Depts. Huánuco, Pasco, and Junín, in Peru. Short-tubed plants, including the types of *F. hirsuta* and *F. unduavensis,* grow at higher elevations, either as epiphytes or more frequently terrestrially along banks or among rocks; these

plants occupy a wider range, from Dept. San Martín in Central Peru to Dept. Cochabamba in Bolivia. Very few specimens with intermediate tube lengths have been collected; *Macbride 4901,* with tubes 85 mm long, and *Macbride 4970,* with tubes 70–120 mm long, both from Dept. Huánuco in Peru, were the only such sheets seen. On the other hand, both short- and long-tubed plants have been found to occur in the same general area; in Dept. Junín, between Concepción and Satipo, individuals with floral tubes 6 cm long were found growing out of road banks at 3,600 m, 123–133 km west of Satipo (*Berry & Aronson 3068, 3069*). Further east along the same road, plants with floral tubes 12–13 cm long were found as epiphytes on *Blechnum* trunks, at 3,350–3,400 m, 72–73 km west of Satipo (*Berry & Aronson 3070, 3071*). Except for the difference in the tube length, the two populations are very similar in characters such as coloration, pubescence, tube shape, knotty stems, and leaf type; interestingly, the sepals are approximately the same size and shape in both populations, unlike the large, flaring sepals shown in the short-tubed plant in Ruiz and Pavón's illustration. Before deciding whether two distinct taxonomic entities should be recognized for the short-tubed and the long-tubed plants, it will be necessary to undertake more intensive collections in central Peru, where both forms and possibly some with intermediate tube lengths occur.

Three different short-tubed populations of *F. apetala* were examined cytologically, and all were tetraploid ($n = 22$). The only other tetraploids known in sect. *Hemsleyella* are the distantly related *F. juntasensis* and in a population of possible hybrids (× *F. inflata*) in eastern Peru. Although no counts were obtained from long-tubed plants of *F. apetala, Berry & Aronson 3071* has a large percentage of triporate pollen grains, a character generally associated with polyploidy in the genus (Praglowski et al., 1983; Nowicke et al., 1984).

A number of collections are doubtfully referred to *F. apetala* because they differ from the description and general characters of the species in one or more traits. Two of these are long-tubed plants from Ampay, Dept. Apurimac, Peru, that cannot be unequivocally placed either in *F. inflata* or *F. apetala. Vargas 1000* (BH, CUZ, GH, UC, 10 June 1938, 3,200–3,500 m) has floral tubes 11–12 cm long, which are pilose, yet ampliate as in *F. inflata* (10–16 mm diam. in the middle of the tube); the leaves, however, are large and ovate-cordate, as in *F. apetala.* The second collection from Ampay, *Marín 2253* (F, July 1950, 3,600 m), has subcylindric, pilose floral tubes 90–105 mm long and ovate leaves, but lacks the knotty stems typical of *F. apetala. Dudley 11215B* (NA, 19 July 1968, Peru, Dept. Cuzco, Prov. La Convención, ca. 25 km NE of Hda. Luisiana and Río Apurimac) is a fairly typical short-tubed example of *F. apetala,* except for its very large and broad sepals 36 mm long by 17 mm wide. *Berry & Aronson 3014* (MO, 21 July 1978, Peru, Dept. Cuzco, Prov. Quispicanchis, 3,120 m, 91 km from Ocongate above Marcapata) has short, pilose floral tubes and knotty stems, but the tubes are more constricted than is usual in *F. apetala,* and the collection was diploid, $2n = 22$. *Chávez 3489* (MO, 12 Nov. 1976, Peru, Dept. Cuzco, Quebrada Las Peñas, 3,150 m, 10 dm tall in rock fissures) is a plant with somewhat knotty stems and moderately ampliate floral tubes, yet the flowers have fine, whitish pubescence and pink sepals, and it is seemingly intermediate between *F. apetala* and *F. tunariensis.*

Another group of old collections, presumably all from central Peru, recall the illustration that accompanies Ruiz and Pavón's type description of *F. apetala. Lobb s.n.* (K) has rather ampliate tubes 46–48 mm long, large and broad ovate sepals (18 mm long, 9 mm wide), smooth stems, and large leaves 13 cm long and 8 cm wide. *Lobb 112* (K, W, from Muña, Dept. Huánuco) has similar flowers, with tubes 58–60 mm long, sepals 21 mm long and 10 mm wide, and filaments 17–20 mm long. Similar collections are *Gay,* 1839–1840 (P), but with very pilose leaves and knotty stems, and *Dombey s.n.* (F), from "Churupallana," with petioles to 6 cm long. It is possible that these collections correspond to Ruiz and Pavón's illustration accompanying the type description of *F. apetala* and that they represent a yet undescribed apetalous species from the Huánuco-Pasco region, most closely resembling *F. insignis* from Ecuador. Further field work will be necessary to determine if this is so.

2. **Fuchsia cestroides** Schulze-Menz, Notizbl. Bot. Gart. Berlin-Dahlem 15: 137. 1940. Macbride, Field Mus. Nat. Hist., Bot. Ser. 13: 550. 1941. Munz, Proc. Calif. Acad. Sci., Ser. 4, 25: 83, pl. 14, fig. 74. 1943. TYPE: Peru. Dept. Piura: Prov. Ayavaca, W slopes

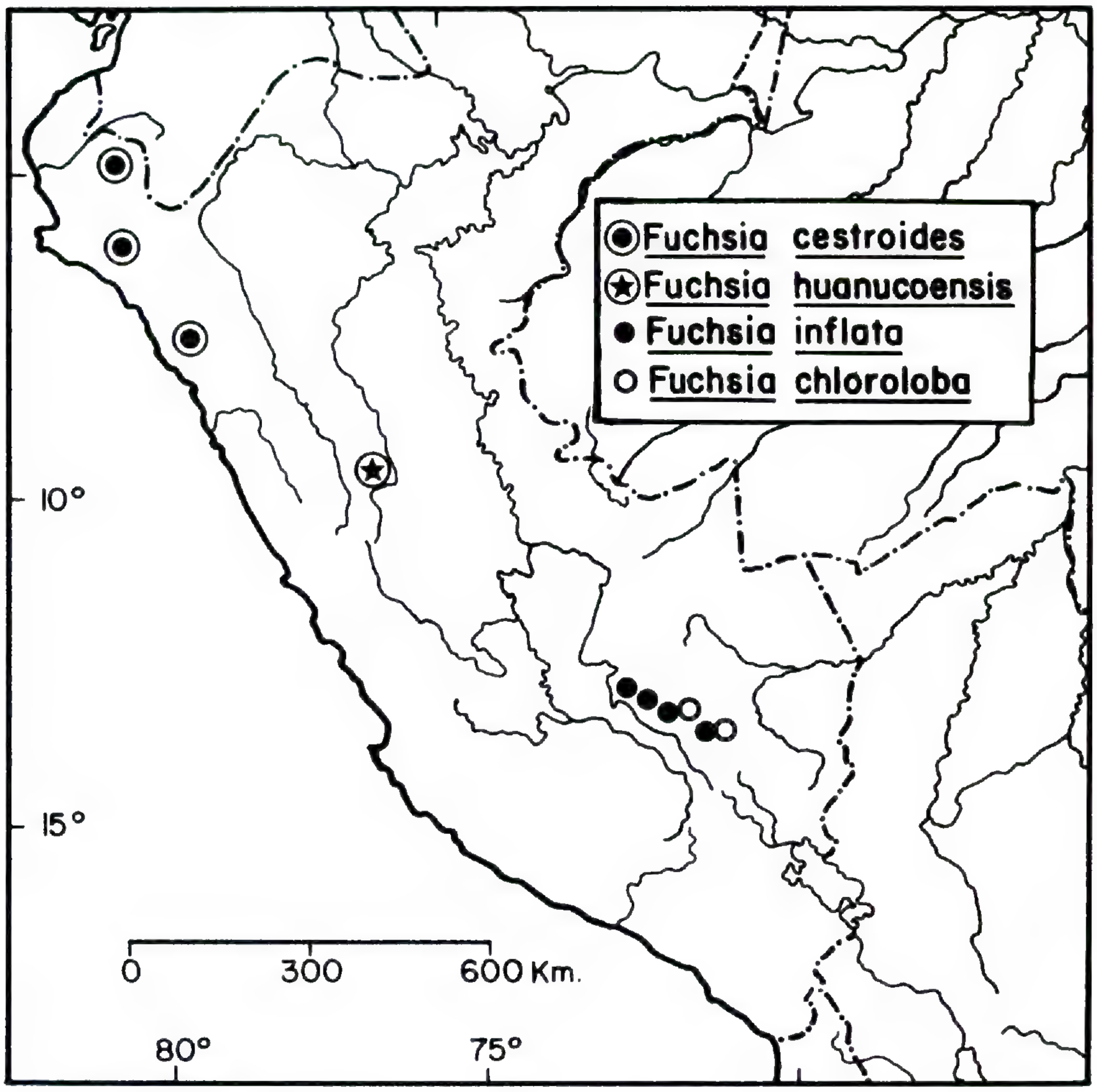

FIGURE 11. Distribution of the species of *Fuchsia* sect. *Hemsleyella* restricted to Peru.

of the Andes below Frias, 1,000–1,200 m, 21 May 1912, *Weberbauer 6423* (holotype, B, destroyed in World War II; isotypes, F—2 sheets, GH, US; photographs of US isotype, BH, NY, UC).

Erect to scandent shrubs 0.5–3 m tall. Branchlets terete, 1.5–3 mm thick, puberulent to pilose; older stems 5–40 mm thick, with exfoliating bark. Leaves opposite or ternate, membranous, elliptic, 26–100 mm long, 14–15 mm wide, apex and base acute, subglabrous to puberulent above, puberulent below, especially on the veins; margin subentire to serrulate, secondary veins 6–14 on either side of the midvein. Petioles strigose, (2–)4–8 mm long. Stipules lanceolate, ca. 1 mm long, ca. 0.5 mm wide. Flowers generally numerous on terminal and axillary racemes with small, deciduous, lance-filiform bracts; rachis (15–)25–35 mm long. Pedicels puberulent, 3–4 mm long. Ovary cylindrical, 3–4 mm long, 1–1.5 mm wide, puberulent to pilose. Floral tube narrowly funnelform, 18–20 mm long, 2–3 mm wide at the base, narrowed to ca. 1.5 mm wide in the lower ⅓, then gradually widened to ca. 4 mm wide at the rim, lightly puberulent to pilose outside, retrorse villous inside in lower ⅓. Sepals oblong-lanceolate, 5–7 mm long, 2.5–3 mm wide, obtuse to acute at the apex, connate for ca. 1.5 mm at the base, spreading at anthesis. Tube rose pink to lavender, sepals greenish (in bud) to dull purple. Nectary ca. 3 mm high. Filaments green, the antesepalous ones 3.5–6(–7) mm long, the antepetalous ones 2–5 mm long; anthers broadly elliptic, yellow, ca. 1.5 mm long, ca. 1 mm wide. Style glabrous, exserted 5–8 mm beyond the anthers. Stigma clavate, 1.5–2 mm long, ca. 1 mm wide, slightly 4-cleft at the apex. Immature fruit oblong, 8 mm long, 5 mm wide, with ca. 50 seeds. Gametic chromosome number, $n = 11$.

Distribution. Northwestern Peru. Rare and endemic to scrub vegetation between 1,100 and 1,700 m on the Pacific-facing slopes of the Andes in Depts. Cajamarca, Lambayeque, and Piura. Figure 11.

Specimens examined. PERU. CAJAMARCA: Andaloy, between San Benito and Guzmango, 1,600–1,800 m, *Berry et al. 3600* (liquid-preserved specimen, author's collection), *López & Sagástegui 6251* (US). LAMBAYEQUE: Prov. Lambayeque, ca. Km 29 E of Olmos, between Olmos and Jaen on Mesones-Muro highway, 1,150 m, *Hutchison & Wright 3408* (RSA, UC).

This is an extremely rare species that is somewhat unusual for the section. Indeed, Munz (1943) remarked that in its shrubby habit, opposite-ternate, elliptic leaves and dense inflorescences of small flowers, the type specimen of *F. cestroides* resembled fairly closely certain species in sect. *Fuchsia,* such as *F. lehmannii.* Nonetheless, the lack of petals and the band-type nectary clearly place it in sect. *Hemsleyella.* Geographically, *F. cestroides* is strongly isolated from other members of the section, by inhabiting the rather dry, open scrub vegetation of the Pacific slopes of the northern Andes of Peru.

The small number of specimens collected makes it difficult to assess the degree of variability in vegetative characters in *F. cestroides.* Both collections from Cajamarca were leafless when collected in flower, and the leaves present on *Hutchison & Wright 3408,* from Lambayeque, are quite distinct from those of the type specimen: they are opposite, semicoriaceous, smaller (30 mm long, 15 mm wide), with obtuse tips and petioles just 2–3 mm long. Further collections from the northwestern departments of Peru may eventually show that these specimens belong to a different taxon from *F. cestroides,* but one that is related to it.

3. Fuchsia chloroloba Johnston, J. Arnold Arbor. 20: 243. 1939. TYPE: Peru. Dept. Cuzco: Prov. Paucartambo, Pillahuata, Cerro de Cusilluyoc, 2,200–2,400 m, 3–6 May 1925, *Pennell 13973* (holotype, GH, photograph at NY; isotypes, F, NY, PH). Figure 12.

Fuchsia tuberosa sensu Macbride, Publ. Field Mus. Nat. Hist., Bot. Ser. 13: 564. 1941, pro parte.
Fuchsia tuberosa Krause var. *typica* sensu Munz, Proc. Calif. Acad. Sci., Ser. 4, 25: 76, pl. 12, fig. 66. 1943, pro parte.

Shrubs 1–2 m high, usually growing in rocks or epiphytic on trees, with globose to ellipsoid tubers 1–4 cm thick. Branchlets terete, smooth, purplish, 1.5–5 mm thick; older stems 0.5–2 m long, 5–18 mm thick, with freely exfoliating bark. Leaves alternate, usually lacking at anthesis, membranous, narrowly lance-ovate, 60–120 mm long, 20–55(–60) mm wide, apex acuminate, base cordate to subcordate, glabrous on both sides; margin subentire to remotely denticulate, secondary veins 5–9 on either side of the midvein. Petioles 14–45 mm long. Stipules filiform, ca. 2 mm long, 0.2–0.3 mm wide, deciduous. Flowers few to numerous, axillary or clustered at the tips of young shoots. Pedicels dull red or green, 26–60(–70) mm long. Ovary (narrowly) cylindric, 10–24 mm long, 2–4 mm wide, lustrous light green. Floral tube (38–)41–51 mm long, 4–5 mm wide and bulbous at the base, thereupon strongly constricted to 1.5–2 mm wide in the lower ⅓–¼ of the tube, then abruptly widened until 10–13.5 mm wide in the upper half before narrowing slightly to 9–11(–12) mm wide at the rim, glabrous outside, pilose inside in the lower ¼. Sepals lance-ovate, thin membranous, 16–24 mm long, 5–10(–12) mm wide, apex acute to acuminate, connate for 5–7 mm at the base, tetragonous in bud, spreading-divergent at anthesis. Tube glaucous, bright scarlet to light orange-pink, sepals parrot green. Nectary 6–8 mm high. Filaments green, the antesepalous ones 10–16 mm long, the antepetalous ones 8–13 mm long; anthers oblong, yellow, 4–5 mm long, 2–3 mm wide. Style pale green, pilose inside in the lower ⅓; stigma clavate, green, 4–4.5 mm long, ca. 2 mm wide, exserted 5–15 mm beyond the anthers. Mature berry not seen. Gametic chromosome number, $n = 11$.

Distribution. Southern Peru, endemic to cloud forest in several valleys in Prov. Paucartambo and Prov. Quispicanchis, Dept. Cuzco, (1,600–) 2,200–2,800 m. Flowers in the dry season, principally from May to October. Figure 11.

Specimens examined. PERU. CUZCO: Prov. Paucartambo, just above Buenos Aires, Km 131–132 on Cuzco-Paucartambo-Pilcopata road, *Berry et al. 2599* (MO—2 sheets); Km 120 from Cuzco to Pilcopata, just above upper tunnel, *Berry et al. 3008* (MO—2 sheets); Prov. Quispicanchis, above Marcapata, 92 km from Ocongate, *Berry & Aronson 3015* (MO, USM), *3024* (MO, USM); 2 km below Opispata, near Marcapata, *Berry & Aronson 3017* (MO, USM), *Metcalf 30719* (A, MO, UC, US), *Rauh P1282* (RSA), *Vargas 6214* (CUZ), *16567* (CUZ), *Wasshausen & Encarnación 783* (MO); Prov. Paucartambo, Tambomayo, *Vargas 60* (CUZ—2 sheets, F, MO); Pillahuata, Paso del Aguila, *Vargas 16764* (CUZ), *22997* (MO); Prov. Paucartambo, Achirani, Marcachea, *Vargas 1625* (CUZ, MO); between Achirani and Medias-Mayu, *Vargas 11116* (A, F, G-DEL, K, NA, UC); Cosuepata, Prov. Paucartambo, *Velarde 1197* (RSA); Prov. Paucartambo, Río Tambomayo, from Pillahuata Bridge to head of Tambomayo Grande; *West 7094* (GH, MO—2 sheets). CULTIVATED: Berkeley, California, *Univ. California Bo-*

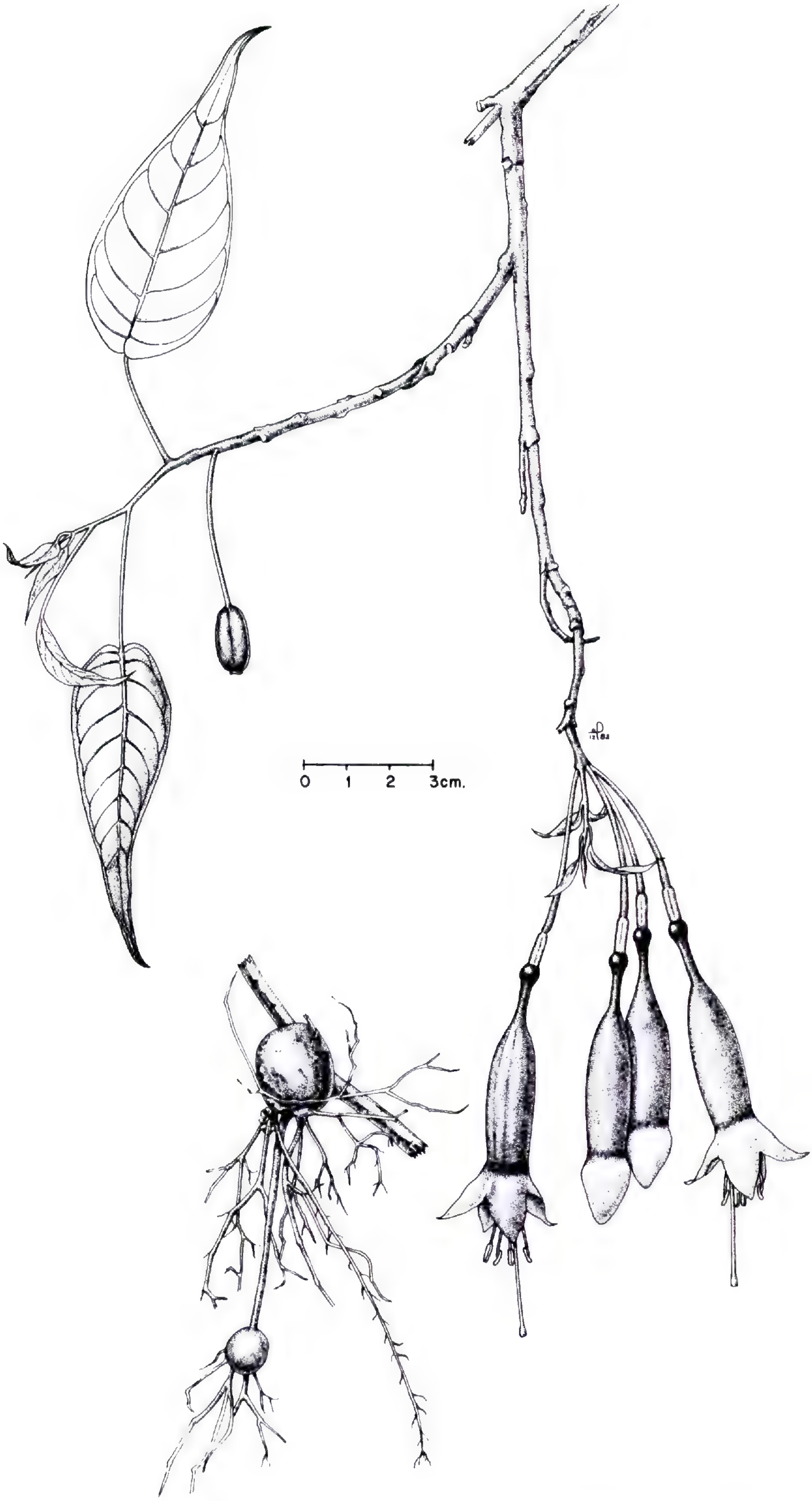

FIGURE 12. *Fuchsia chloroloba,* leafy and flowering branch from *Wasshausen & Encarnación 783,* Prov. Quispicanchis, Dept. Cuzco, Peru; tubers from *Berry et al. 2599,* Prov. Paucartambo, Dept. Cuzco, Peru.

tanical Garden Accession N° 36.1901, from seed of *West 7094,* in 1939 (UC).

This is a very localized and distinctive species, characterized by its short, tubular floral tubes with a very marked constriction in the lower third and a very striking color pattern, with glaucous, orange floral tubes and parrot green sepals. *Fuchsia chloroloba* is highly seasonal, forming well-developed tubers and flowering in the dry season, when most of the leaves are absent. This species has been confused by Munz (1943) with *F. inflata,* with which it grows sympatrically above Marcapata in Prov. Quispicanchis. The latter species has a similar floral tube shape, but the flowers are much longer (without apparent intergradation) and are reddish pink instead of orange, with the sepals less entirely green, as in *F. chloroloba.* Nonetheless, it is possible that natural hybrids occur between the two taxa, as described in the section on Sympatry and Hybridization.

4. Fuchsia garleppiana Kuntze & Wittmack, Gartenflora 42: 461, fig. 96. 1893. Munz, Proc. Calif. Acad. Sci., Ser. 4, 25: 82, pl. 14, fig. 72. 1943. TYPE: Bolivia. Dept. Cochabamba: cloud forest at Cocapata, Tunari Range, 3,000 m, Apr. 1982, *Kuntze* (holotype, NY; isotypes, F-297181, F-297182, NY, photographs of F-297182 at NY, UC). Figure 13.

Shrubs 0.5–4 m tall, growing epiphytically or more commonly out of rock crevices, with strongly developed cylindrical tubers 10–80 cm long and 2–4 cm thick and more or less erect branches 1–2.5 m long. Young growth densely white-pilose; branchlets terete, 2–4 mm thick, red-green; older stems 4–10 mm thick, with freely exfoliating bark. Leaves alternate, usually absent at anthesis, membranous, ovate to elliptic-ovate, mature blades 90–130 mm long, 55–75 mm wide, apex subacuminate, base rounded to cordate, light green and subglabrous above, pilose along veins and margin below; margin subentire to remotely denticulate, secondary veins 9–10 on either side of the midvein. Petioles pilose, 40–73 mm long on mature leaves. Stipules filiform, ca. 2 mm long, deciduous. Flowers few to many, axillary or grouped at branch tips. Pedicels densely pilose, greenish pink, 7–30(–60) mm long. Ovary narrowly cylindric, 7–8 mm long, 2–2.5 mm thick, densely pilose. Floral tube narrowly tubular-funnelform, (45–)70–140 mm long, 3.5–6(–7) mm wide and bulbous at the base, then constricted to 2–2.5 mm wide and gradually widened above until 7–10 mm wide below the slightly constricted mouth, pilose outside, villous inside for most of length. Sepals lance-ovate, 10–18 mm long, 5.5–7(–8) mm wide, apex acute, connate for ca. ⅓ of length at the base, spreading-divergent at anthesis. Tube and sepals light to very pale pink, with a dark purple ring on the throat where the stamens are inserted. Nectary lustrous green-purple, 4–6 mm high. Filaments green, the antesepalous ones 10–12 mm long, the antepetalous ones 8–9 mm long; anthers yellow, 3–4 mm long, 1.5–2 mm wide. Style light pink, villous for most of length; stigma green, globose, 2–2.5 mm long, 2.5–3 mm wide. Young berries narrowly cylindric, ca. 22 mm long, ca. 4 mm wide. Gametic chromosome number, $n = 11$.

Distribution. Endemic to cloud forest in Dept. Cochabamba, Bolivia, at 2,500–2,950 m. Flowers principally in the dry season, when leafless, from (March to) April to August. Figure 10.

Specimens examined. BOLIVIA. COCHABAMBA: Prov. Chapare, 54 km towards Villa Turari, *Beck 1414* (MO—2 sheets); 41–42 mi. from Cochabamba to Chapare, *Berry & Berry 2582* (MO—2 sheets); *2583* (MO—2 sheets), *2590* (MO); 5 km from Incachaca on old road to Aguirre, *Berry 3635* (MO). Incachaca, road to Aguirre, *Brooke 6741* (BM, F, G-DEL, NY, S, U); Incachaca, *Cárdenas 688* (US); near Chulumani, way to Yungas de Tablas, *Cárdenas 6279* (NY, US); way to Río Chulumani, mule path to Yungas de Tablas, *Cárdenas s.n.* (POM); Incacorral-Aduana, *J. Steinbach 9538* (BM, F, G-DEL, GH, K, MO, NY, PH, S, U, Z).

Of all the native Bolivian fuchsias, *F. garleppiana* is the only one with floral tubes over 7 cm long. It is also characterized by the very pale pink coloration of the flowers, the dense white-pilose pubescence on the young growth, and its primarily shrubby habit. Although this species has well-developed, cylindrical tubers and flowers in the dry season when it is leafless, it is rarely truly epiphytic; rather, it prefers exposed rocks, from which erect stems to 1 m tall emerge. Only two other species of *Fuchsia,* both from Peru, can have similarly long flowers; *Fuchsia apetala* is basically epiphytic or terrestrial at higher elevations, with creeping, tortuous stems and reddish orange flowers. *Fuchsia inflata,* the other species with long floral tubes, sometimes has a habit similar to that of *F. garleppiana,* but its floral tubes are pink-orange, much more constricted at the base and broader at the top, and it has yellow-green sepals.

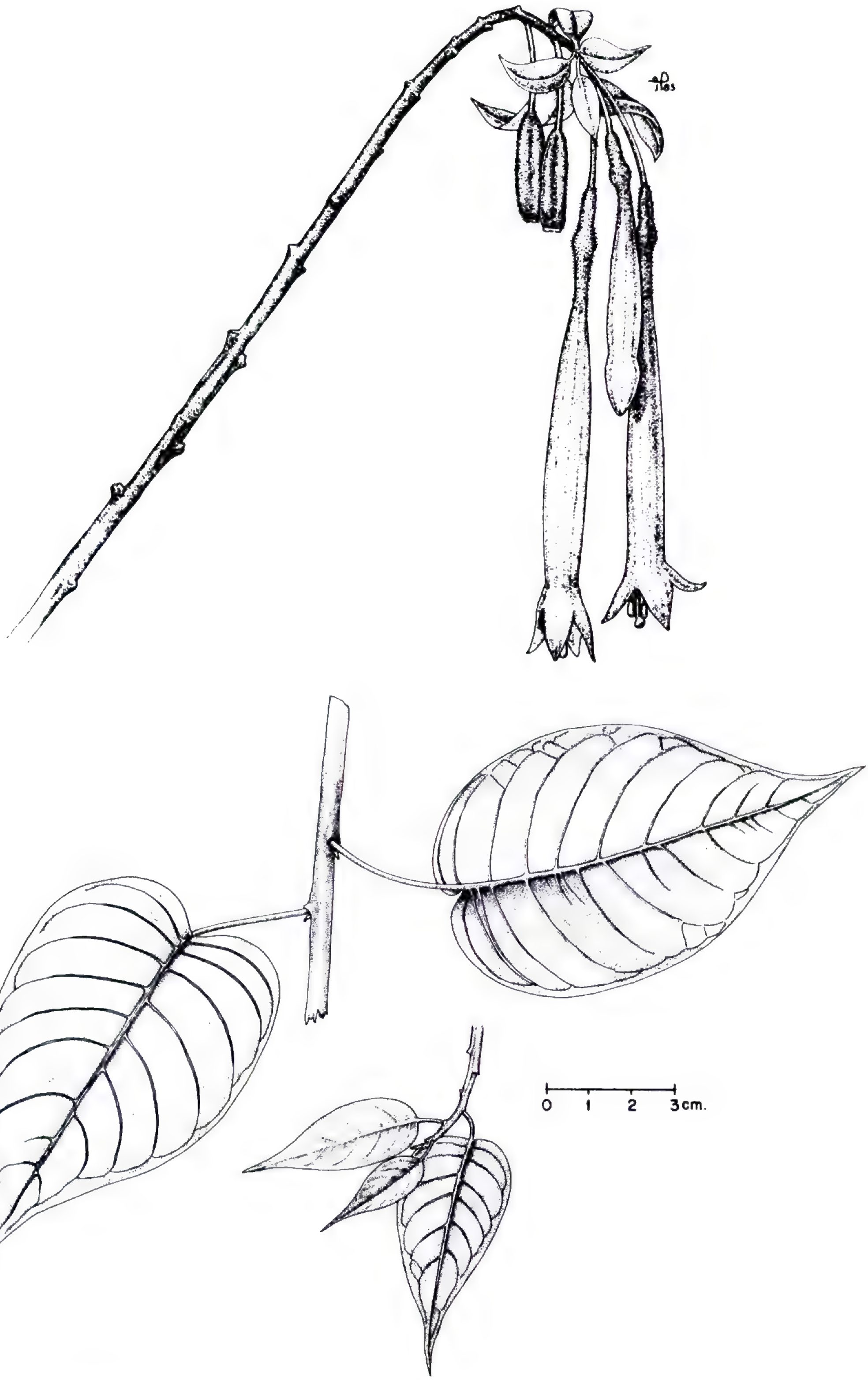

FIGURE 13. *Fuchsia garleppiana*, flowering branch from *Berry & Berry 2583*, Dept. Cochabamba, Bolivia; leaves from *Beck 1414*, Dept. Cochabamba, Bolivia.

5. Fuchsia huanucoensis P. Berry, sp. nov. TYPE: Peru. Dept. Huánuco: Carpish Divide, Chinchao Valley, 8,500 ft., Oct. 1945, *Sandeman 5166* (holotype, K; isotypes, K, OXF).

Frutex scandens, ramis oppositis. Folia coaetanea, opposita, firme membranacea, anguste elliptico-ovata, apice subacuminata, basi acuta vel rotundata, 40–80 mm longa, 18–30 mm lata, petiolis 6–10 mm longis. Flores pauci axilaresque ad apicem ramorum, pedicellis gracilibus cernuis 24–35 mm longis. Tubi florales anguste infundibuliformes, 31–34 mm longi, basi ca. 3.5 mm lati inde gradatim dilatati summo ca. 7 mm lati. Sepala anguste lanceolata, apice anguste acuta vel acuminata, 22–23 mm longa, 4–5 mm lata, basi connata 2–3 mm limbis sub anthesi valde patentibus.

Low, scandent shrubs with oppositely branched stems. Branchlets subterete, 1–3 mm thick, purplish, pilose with white hairs; older branches pilose, with lustrous purple bark splitting longitudinally. Leaves present at anthesis, opposite, firmly membranous, narrowly elliptic-ovate, 40–80 mm long, 18–30 mm wide, apex subacuminate, base acute to rounded, apparently dark green and subglabrous above, paler below with pilose midvein and margin; margin subentire, secondary veins 6–10 on either side of the midvein. Petioles strigose, purplish, 6–10 mm long. Stipules lance-triangular, 1–1.5 mm long, deciduous. Flowers few and axillary, close to the branch tips. Pedicels slender, drooping, sparsely pilose, 24–35 mm long. Ovary oblong, 6–7 mm long, ca. 3 mm wide. Floral tube narrowly funnelform, 31–34 mm long, ca. 3.5 mm wide at the base, then gradually widened above until ca. 7 mm wide at the rim, subglabrous outside, pilose inside in lower ½. Sepals narrowly lanceolate, apex narrowly acute to acuminate, 22–23 mm long, 4–5 mm wide, connate for 2–3 mm at the base, tips strongly spreading or recurved at anthesis. Tube and sepals magenta or bright reddish pink. Nectary ca. 3 mm high. Filaments reddish, the antesepalous ones 13–20 mm long, the antepetalous ones 9–14 mm long; anthers narrowly oblong, 3–4 mm long, ca. 2 mm wide. Style reddish, pilose for most of length; stigma subclavate, barely 4-cleft at the apex, ca. 2 mm long, ca. 1.5 mm wide. Berry not seen.

Distribution. Central Peru, known only from the type locality in cloud forest at the Carpish Divide, Dept. Huánuco, 2,750–2,950 m. Is known to flower from October to November. Figure 11.

Specimen examined. PERU. HUÁNUCO: Carpish, 9,000 ft., *Sandeman 3480* (K).

This species is allied to *F. juntasensis, F. membranacea,* and *F. tillettiana,* by virtue of its fruticose habit, opposite and narrowly ovate leaves, apparent lack of tubers, medium length flowers, and reflexed sepals. It is readily distinguished from these species, however, by its firmer, narrower leaves, with sparse pilose pubescence, narrowly lanceolate sepals, and disjunct distribution. *Fuchsia huanucoensis* is apparently very rare, as the Carpish area has been relatively well collected by botanists.

6. Fuchsia inflata Schulze-Menz, Notizbl. Bot. Gart. Berlin-Dahlem 15: 136. 1940. *Fuchsia tuberosa* Krause var. *inflata* (Schulze-Menz) Munz, Proc. Calif. Acad. Sci., Ser. 4, 25: 77. 1943. TYPE: Peru. Dept. Cuzco: Prov. Paucartambo, above Cosñipata, between Tambo Tres Cruces and Tambomayo, 3,100 m, 25 Apr. 1914, *Weberbauer 6935* (holotype, B, destroyed in World War II; isotypes, F—2 sheets, GH, POM, US—2 sheets). Figures 1–4, 14.

Fuchsia macrantha sensu Munz, Proc. Calif. Acad. Sci., Ser. 4, 25: 83, pl. 14, fig. 73. 1943, pro parte.

Shrubs 1–3 m high, usually growing among rocks, or epiphytic on trees, with well-developed, cylindrical, tan tubers 2–50 cm long and 2–4 cm thick. Branchlets terete, 2–5 mm thick, tan to reddish, glabrous to densely cinereous or velutinous; older stems erect to divergent and 1–3 m long, 4–12 mm thick, with freely exfoliating bark. Leaves alternate or rarely opposite, membranous, narrowly elliptic to ovate, 55–135 mm long, 20–52 mm wide, apex acuminate, base acute to rounded or subcordate, glabrous to sparsely pubescent above, glabrous to pubescent along the veins below; margin subentire to remotely denticulate, secondary veins 6–9 on either side of the midvein. Petioles glabrous to canescent-velutinous, 12–22(–35) mm long. Stipules filiform, 1.5–2 mm long, deciduous. Flowers axillary, one or few to numerous, usually densely clustered at branch tips. Pedicels pale green to reddish, 20–55(–70) mm long, glabrous to densely pubescent. Ovary ellipsoid to narrowly cylindrical, 8–18 mm long, 2–3 mm wide, subglabrous to densely cinereous, sometimes 8-sulcate. Floral tube 85–120 mm long, 5–9 mm wide and strongly bul-

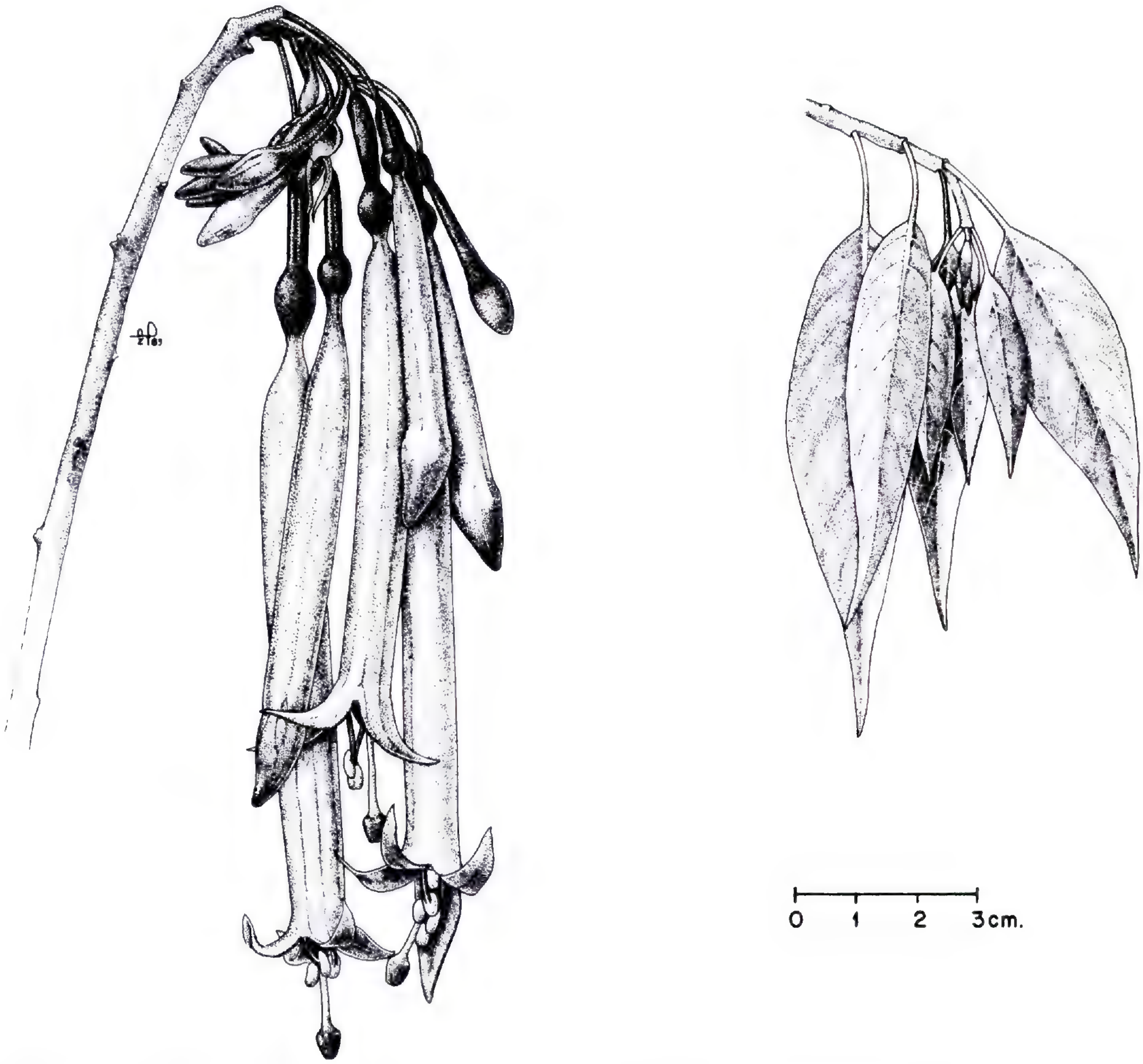

FIGURE 14. *Fuchsia inflata*, flowering branch from *Berry & Aronson 3036*, Prov. La Convención, Dept. Cuzco, Peru; leaves from *Vargas 23044*, Prov. Calca, Dept. Cuzco, Peru.

bous at the base, strongly constricted to 2–4 mm wide above the nectary, then abruptly widened to (8–)10–14 mm wide in the upper part of the tube, slightly constricted to 7–12 mm wide at the mouth, glabrous to densely canescent or pilulose outside, pilose inside on lower ⅓. Sepals narrowly triangular to lanceolate, 15–26 mm long, 6–10 mm wide, apex acute, connate for 4–10 mm at the base, somewhat recurved at anthesis or divergent in lower ½ and suberect in upper ½. Tube (light) pink to orange, the base greenish or dull purple around the nectary, sepals light green to dull yellow-green. Nectary 3–5 mm high. Filaments green to pale yellow-green, the antesepalous ones 15–20 mm long, the antepetalous ones 8–16 mm long; anthers (narrowly) oblong, yellow, 4–5 mm long, 2–3.5 mm wide. Style green to white-yellow, villous in lower ½ or for most of length; stigma green, clavate to globose, sometimes tetragonous, 4-cleft at the apex, ca. 4 mm long, 2–3 mm wide. Young berries 20–40 mm long, 5–6 mm wide. Gametic chromosome number, $n = 11$.

Distribution. Dept. Cuzco, Peru, endemic to several valleys on the eastern slopes of the Andes, (2,350–)2,850–3,600 m. Flowers principally in the dry season, from June to August. Figure 11.

Specimens examined. PERU. CUZCO: Prov. Convención, Km 145–146 from Cuzco to Quillabamba, *Berry & Berry 2567* (MO), *2568* (MO), *2569* (MO), *2570* (MO), *Berry & Aronson 3036* (MO, USM), *3037* (MO), *3038* (MO, USM), *Gentry 19830* (MO); Km 150 on Cuzco-Quillabamba road, *Berry & Aronson 3040* (MO); Km 156 on Cuzco-Quillabamba road, *Berry &*

& Berry 2572 (MO); Prov. Quispicanchis, Km 88–92 from Ocongate to Marcapata, *Berry & Aronson 3010* (MO), *3011* (MO), *3012* (MO), *3013* (MO), *3016* (MO); across river from Marcapata, *Berry & Aronson 3023* (MO—2 sheets); Quillabamba, Sta. Teresa, 0.5 km W of La Playa at Mandornilloc, *Peyton & Tilney-Peyton 1274* (MO); Rio Marcapata, *Rauh & Hirsch P1308* (RSA); Prov. Calca, around Lares, *Vargas 3595* (BH—2 sheets); Prov. Calca, Amparaes, *Chávez 3273* (MO), *Vargas 23044* (MO); Prov. Convención, Lucumayo Valley, *Cook & Gilbert 1312* (US); Prov. Calca, near Lares, *Vargas 3584* (BH, CUZ, MO), *3595* (BH, CUZ); Prov. Convención, Yanamache-Lucumayo, *Vargas 4451* (CUZ—2 sheets); near town of Marcapata, *Vargas 11687* (CUZ); Prov. Calca, between Amparaes and Km 68, *Vargas 15581* (CUZ); Prov. Urubamba, above ruins of Machupichu, *Vargas 19901* (CUZ); without locality, *Weddell,* 1847 (F); Yanatili, *Weibel,* 1976 (USM). CULTIVATED: Berkeley, California, flowering in summer of 1940, *Univ. Calif. Botanical Garden Accession N° 38.1052,* from Dept. Cuzco, Peru (UC).

A complex pattern of variation occurs in the long-tubed plants of sect. *Hemsleyella* that inhabit a series of adjacent valleys to the north, east, and west of the city of Cuzco, in southern Peru. An adequate understanding of the intra- and interpopulational variability of this group, here treated as belonging to one species, *F. inflata,* has not been possible, because of the scarcity of these plants, their strong seasonality and an insufficient sampling of the populations in each of the valleys.

In general, the specimens treated here under *Fuchsia inflata* can be distinguished by their floral tubes 8–12 cm long, with a bulbous base around the nectary, followed by a narrow constriction before forming a tube that tapers slightly towards the rim. Unlike *F. apetala* and *F. garleppiana,* the only other species in the genus that can have such long-tubed flowers, the sepals of *F. inflata* are mostly green, and the leaves are much narrower than either of the other species. Furthermore, only *F. apetala* has knotty-tortuous stems, and *F. garleppiana* alone has pale pink flowers. Macbride (1941) and Munz (1943) treated specimens of *F. inflata* as long-tubed variants of *F. tuberosa,* for which both of them refer to plants presently recognized as *F. chloroloba.* Although *F. chloroloba* and *F. inflata* can occur sympatrically, and both have marked floral tube constrictions, the floral tubes of the former are quadrangular in cross section, and the tubes never exceed 55 mm in length, while the sepals are entirely parrot green and the tubers are smaller and more spherical than the elongate ones of *F. inflata.*

The type collection of *F. inflata* is the only specimen of this group collected in the Paucartambo Valley, which is in the central part of the range of the species; that specimen is glabrous throughout and bears both opposite and alternate leaves. Other collections agreeing with the type description and the characters noted previously occur to the southeast, along the Río Marcapata. However, in a series of collections made on July 21, 1978 along the Río Marcapata, 88–92 km from Ocongate, at elevations between 3,000 and 3,280 m, considerable differences in flower color, floral tube shape, and leaf size and shape were found among long-tubed plants most closely agreeing with *F. inflata. Berry & Aronson 3010* and *3011* were found just meters apart at 3,280 m, in full sun among rocks and boulders above the river (see Fig. 4); *3010* had green sepals and light pink floral tubes sharply constricted at the base but broad above and was leafless, whereas *3011* had numerous large leaves, yellowish sepals and much narrower, less constricted floral tubes. Fifty meters downriver, *Berry & Aronson 3013* had flowers similar in shape to *3010,* but with salmon orange floral tubes. At 3,120 m, 1 km below *3013,* an odd plant with floral tubes 50 mm long and with knotty stems similar to *F. apetala* was found, *Berry & Aronson 3014.* Just 20 m below, *F. chloroloba* appeared. Chromosome counts were obtained from several of these plants, yielding n = ca. 22 for *3010,* $2n = 44$ and n = ca. 22 for *3011,* $2n = 22$ for *3014,* and $n =$ 11 for *3015.* Anaphase I of pollen mother cells in *3011* showed meiotic irregularities such as bridges and chromosome fragments. It is unclear what is occurring in this area, but some hybridization may have resulted among entities assignable to *F. inflata, F. chloroloba,* and possibly *F. apetala.*

The remaining specimens cited here under *F. inflata* come from valleys further to the northwest, in the Provinces Calca and La Convención (with a single collection from Prov. Urubamba). Although they all have leaves and floral tubes similar in size and shape to the plants described as "typical" for this species, they differ noticeably in their much longer, slender ovaries (to 4 cm long in fruit) and in the presence of a fine, ashy canescent pubescence on leaves, stems, and flowers, including the interior of the sepals in some cases. In addition, both the ovaries and the bulb around the nectary are sometimes 8-ridged and purplish. As in the populations from Prov. Quispicanchis, however, flower color varies from pink tubes with yellowish sepals (*Berry & Berry 2567*)

to bright orange tubes with mostly light green sepals (*Berry & Berry 2570, 2572,* and *3036*). Two collections examined from this area were both diploid (*Berry & Aronson 3036* and *3040*). Clearly, further cytological information from different populations will be very useful in clarifying the systematics of the *F. inflata* complex.

7. **Fuchsia insignis** Hemsley, J. Bot. 14: 69. 1876. TYPE: Ecuador. Provinces Cañar and Chimborazo: in mossy forest on W slopes of Mt. Azuay, 23–26 Aug. 1859, *Spruce 5976* (lectotype, K—Bentham Herbarium, here designated; isolectotypes, BM, CGE, F, G-BOIS, G-DC, K—Hooker Herbarium, LE, NY, OXF, P—2 sheets, W—3 sheets).

Fuchsia apetala sensu Munz, Proc. Calif. Acad. Sci., Ser. 4, 25: 80, pl. 13, fig. 69. 1943, pro parte.

Scandent or epiphytic vines or shrubs climbing high into trees, or terrestrial shrubs ca. 1 m high. Branchlets smooth, purplish, pilose, 2–5 mm thick, with prominent, alternate leaf scars; older stems freely exfoliating in strips, with stoloniferous runners. Leaves alternate, absent when flowering, membranous, ovate to broadly elliptic-ovate, just two young leaves seen, these 45–90 mm long, 30–40 mm wide, apex acute, base rounded, green and subglabrous above, pale green to purplish and villous below, especially along the veins; margin subentire to remotely denticulate, secondary veins 6–7 on either side of the midvein. Petiole 1–1.5 mm thick, 9–18 mm long. Flowers few to numerous and clustered at the tips of new shoots. Pedicels pilose, 10–23 mm long. Ovary narrowly cylindrical, pilose, 8–10 mm long, 2–3 mm wide. Floral tube funnelform, (38–)40–54(–62) mm long, 4–6 mm wide and bulbous at the base, constricted to 2–2.5 mm in lower ⅓, then gradually widened until 7–11 mm wide at the rim, pilose outside and inside in lower ⅓. Sepals oblong-lanceolate, 24–37 mm long, 7–12 mm wide, usually widest in the middle, apex acute to obtuse, connate for 3–4 mm at the base, strongly recurved at anthesis. Tube and sepals bright scarlet or orange-red. Nectary 4–6 mm high. Filaments green (fide *Rose & Rose 22230*), the antesepalous ones 30–40 mm wide, the antepetalous ones 25–35 mm long; anthers oblong, 4–5 mm long, 2–2.5 mm wide. Style densely retrorse villous in the lower ⅓, exserted 10–15 mm beyond the anthers. Stigma globose, ca. 2 mm long and wide. Immature berry narrowly cylindrical, verrucose, 18–20 mm long, 5–7 mm wide.

Distribution. Southern Ecuador; scarce epiphytes in cloud forest or shrubs on hillsides in Provinces Bolívar, Chimborazo, and Cañar, 2,000–3,240 m. Flowers in the dry season when leafless, mostly from July to October. Figure 15.

Specimens examined. ECUADOR. BOLÍVAR: Chaparro de Gualicón Loma, Cordillera Occidental, *Acosta Solis 6267* (F). CAÑAR: between Cuenca and Huigra, *Hitchcock 21701* (GH, NY, US). CHIMBORAZO: Sibambe, Hda. La Carmela, Sección Era-Pata, Cordillera Occidental, *Acosta Solis 5454* (F); Province of Alausí at 10,000 ft., *Jameson,* 1836 (K); vicinity of Huigra, mostly on Hda. de Licay, *Rose & Rose 22230* (GH, NY, US). WITHOUT PROVINCE: near top of the Cuesta de Angas, on road to Guayaquil, 2 Aug. 1848, *Jameson s.n.* (K); "found in the forest of Camino Real," 8,000 ft., July 1848, *Jameson s.n.* (K); Andes of Ecuador, 9,000 ft., *Pearce s.n.* (K), *Lobb 112* (K).

This species is best distinguished by its unusually large, reflexed sepals and long filaments. It is strongly deciduous, but the presence of tubers in this species has not been noted. No collections of *F. insignis* have been made since 1943, probably a reflection of the destruction of large areas of natural habitat for this species, as well as a possibly brief flowering period and the inaccessibility of the remaining habitats.

8. **Fuchsia juntasensis** O. Kuntze, Revis. Gen. Pl. 3(2): 97. 1898. Munz, Proc. Calif. Acad. Sci., Ser. 4, 25: 77, pl. 12, fig. 67. 1943. TYPE: Bolivia. Dept. Cochabamba: between Cochabamba and Río Juntas, E side of Cordillera, 3,000 m, *Kuntze* (lectotype, NY, here designated). Figure 16.

Fuchsia steinbachii Johnston, Contr. Gray Herb. 75: 38. 1925. TYPE: Bolivia. Dept. Cochabamba: Prov. Chapare, open woods at Incachaca, 2,500 m, 22 Oct. 1920, *Steinbach 5038* (holotype, NY, photograph, UC; isotypes, A, G-DEL).

Terrestrial or commonly epiphytic shrubs 0.5–1.5 m tall, occasionally with small tubers. Young branches purplish, terete, 1–2 mm thick; older branches 4–20 mm thick with bark turning tan and exfoliating in strips or flakes. Leaves opposite or less often ternate, membranous, (narrowly) ovate, 35–110 mm long, 15–50 mm wide, apex acuminate, base acute to rounded, glabrous to sparsely puberulent when young, often purplish below; margin subentire to serrulate, secondary veins 5–7 on either side of the midvein. Petioles 5–9 mm long. Stipules triangular to lanceolate, 2–3 mm long, 1.5–2.5 mm wide, occasionally connate. Flowers few, axillary or grouped

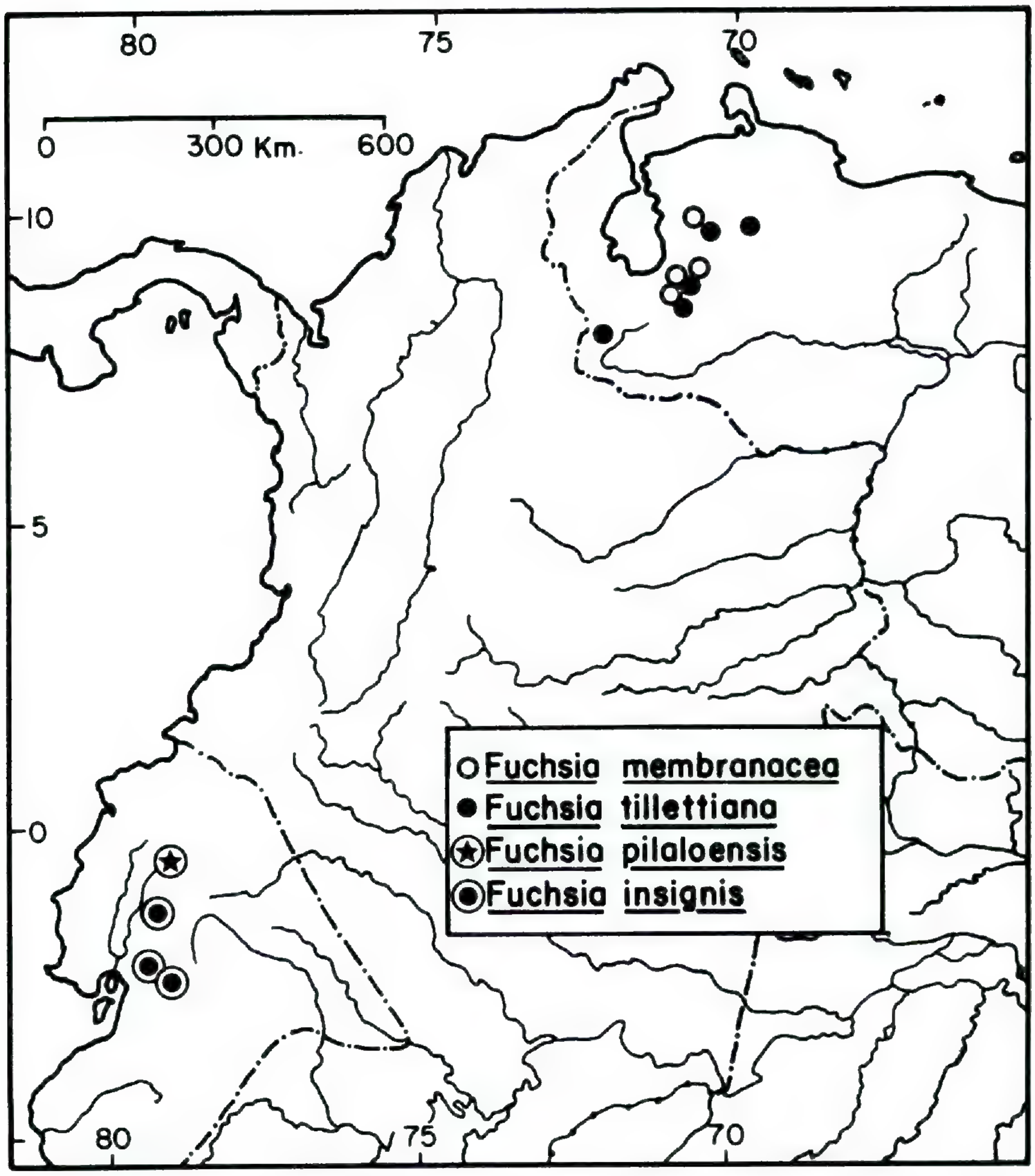

FIGURE 15. Distribution of the Ecuadorian and Venezuelan species of *Fuchsia* sect. *Hemsleyella*.

at branch tips. Pedicels slender, 20–75 mm long. Ovary oblong, greenish, 5–10 mm long, 2–3 mm wide. Floral tube funnelform, 25–50 mm long, 2–4 mm wide at the base, slightly constricted in the lower ⅓, then widened until 8–10 mm wide at the rim, glabrous outside, villous inside in the lower ⅓ above the nectary. Sepals ovate-lanceolate, 14–25 mm long, 4–8 mm wide, apex acute to acuminate, connate for 3–4 mm at the base, divergent to recurred at anthesis. Tube and sepals deep lavender to rose violet. Nectary lustrous green to purplish, 4–5 mm high. Filaments purple, the antesepalous ones 9–21 mm long, the antepetalous ones 6–16 mm long; anthers oblong, yellow, 3–4.5 mm long, 1.5–2.5 mm wide. Style light purple, villous for most of its length; stigma green, 2.5–4 mm long, 2–3 mm wide, 4-cleft at apex, exserted 4–8 mm beyond the anthers. Berry oblong, purplish, 16–18 mm long, 8–10 mm wide (immature). Gametic chromosome number, $n = 22$.

Distribution. Bolivia, restricted to cloud forest on the northeast slopes of the Andes in Dept. Cochabamba, 1,900–2,800 m. Flowers principally in the dry season, from June to October. Figure 10.

Specimens examined. BOLIVIA. COCHABAMBA: Valle de Montepunco, 1,900 m, *Adolfo 380* (US); Valle de Corani, 800 m, *Adolfo 417* (US); 44 mi. from Cochabamba to Chapare, *Berry & Berry 2587* (MO), *2588A* (MO); 4 km above Incachaca on old road to Aguirre, *Berry 3634* (MO); above ENDE pumping station at Corani, *Berry 3638* (MO—2 sheets); Incachaca, *Brooke 6666* (BM, F, NY, U), *6666a* (BM, F, NY, U), *6666c* (BM, F, NY, U), *Cárdenas 2248* (6H), *Werdermann 2030* (MO, S); near Chulumani, road to Yungas de Tablas, *Cárdenas 4089* (F, GH, RSA); cerros de In-

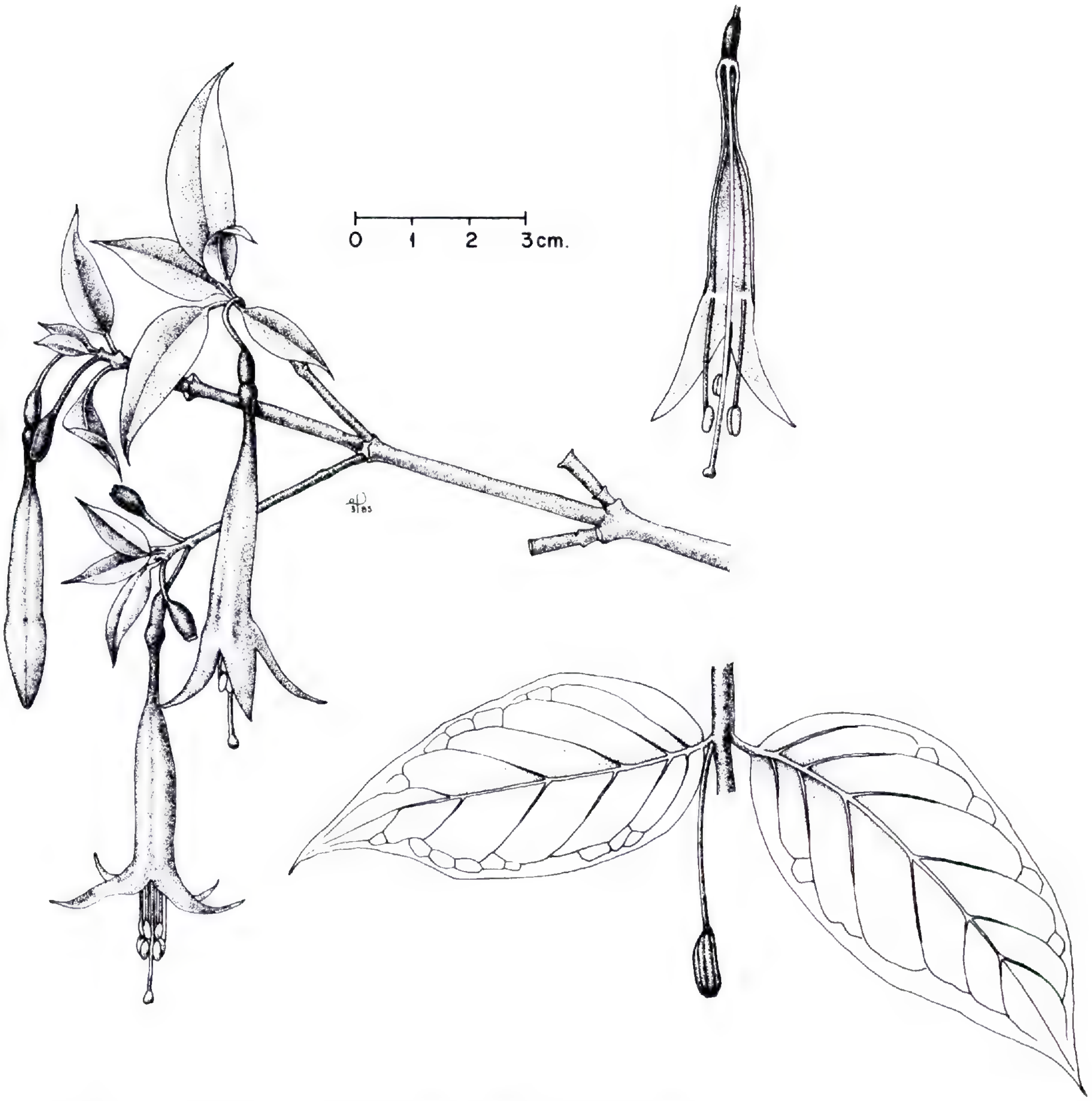

FIGURE 16. *Fuchsia juntasensis*, floral section and flowering branch from *Berry & Berry 2587*, Dept. Cochabamba, Bolivia; leaves from *Berry 3638*, Dept. Cochabamba, Bolivia.

cachaca, *Steinbach 5738* (A, G-DEL, K); Quebrada de Corani, *Steinbach 9862* (BM, F, G-BOIS, K, MO, NY, PH, S, U, UC, Z). WITHOUT LOCALITY: *Bridges s.n.* (BM).

This is one of the opposite-leaved species of sect. *Hemsleyella* with poorly developed tubers; it can be distinguished by its glabrous, mauve or violet-colored flowers, which generally have a lustrous green ovary, a shiny dark purple coloration around the nectary and slightly recurved, lance-ovate sepals. *Fuchsia juntasensis* is known only from the yungas of Dept. Cochabamba in Bolivia, where it occurs as a terrestrial shrub or as an epiphyte. As Brooke (1953) noted, plants of this species found growing in the shade usually flower and produce leaves simultaneously.

A single chromosome count of n = ca. 22 was obtained from *Berry 3638*; curiously, pollen of the same collection is entirely biporate (Praglowski et al., 1983), whereas most other tetraploid plants of *Fuchsia* examined show at least some triporate pollen grains. A possible intersectional hybrid between *F. juntasensis* and *F. denticulata* (sect. *Fuchsia*) is discussed in the section on Sympatry and Hybridization.

9. Fuchsia membranacea Hemsley, J. Bot. 14: 70. 1876. Munz, Proc. Calif. Acad. Sci., Ser.

4, 25: 78. 1943. TYPE: Venezuela. Edo. Mérida: Venta de Mucuchíes, June 1842, *Linden 372* (holotype, K; isotypes, BM, CGE, G-BOIS, G-DC, MICH—fragment from G, MPU—2 sheets, OXF, P—2 sheets). Some labels incorrectly list Caracas, Venezuela as the type locality. Figure 17.

Terrestrial shrubs 1–2 m tall, sometimes climbing to 6 m above ground, growing in rocks, or epiphytic in trees to 10 m above ground; thickened roots to 20 mm thick or small tubers to 2 cm diam. sometimes present. Branchlets red-pink to dark purple, 2–5 mm thick, older stems 5–25 mm thick, with freely peeling, flaky, pale tan bark. Leaves opposite or ternate, sometimes subopposite, membranous, ovate-elliptic, 50–100 mm long, 18–50 mm wide, apex (sub-)acuminate, base rounded to acute, subglossy green and mostly glabrous above, pale green and subglabrous below; margin subentire to denticulate, secondary veins 6–8 on either side of the midvein. Petiole 10–35 mm long. Stipules lance-triangular, 2–2.5 mm long, 1–2 mm wide. Flowers 2–12 per shoot, axillary or grouped toward the branch tips. Pedicels slender, usually green, 30–55(–75) mm long. Ovary cylindrical, 6–7 mm long, 2–4 mm wide, lustrous green or rose-colored. Floral tube funnelform, (30–)36–51 mm long, 2.5–4 mm wide at base, narrowed slightly in lower ⅓, then widened until 7–12 mm wide at the rim, mostly glabrous outside, pilose inside in lower ⅓. Sepals ovate-lanceolate 17–25 mm long, 5–11 mm wide, apex acute, connate for 5–8 mm at base, lobes often split open before anthesis with stigma exserted, spreading at anthesis. Tube red-pink, sepals usually pale green in upper ½. Nectary green, lustrous, 4–5 mm high. Filaments usually green, antesepalous ones 9–15(–20) mm long, the antepetalous ones 7–11 (–16) mm long; anthers oblong, yellow, 3.5–4.5 mm long, 2–3 wide. Style retrorse villous in lower ⅓, exserted 10–15 mm beyond the anthers; stigma clavate, 2.5–3.5 mm long, ca. 2 mm wide, green. Berry cylindrical, 16–18 mm long, 11–12 mm wide, shiny light red when ripe, seeds mostly 60–70 per fruit, triangular-ovate in outline, ca. 2 mm long, 1.3–1.7 mm wide, light brown. Gametic chromosome number, $n = 11$.

Distribution. Venezuelan Andes, in subpáramo and cloud forest in Estados Mérida and Trujillo, (2,600–)2,750–3,400 m. Flowers mostly in the dry season, from January to April. Figure 15.

Specimens examined. VENEZUELA. TRUJILLO: Guiriguay, towards Peñas Blancas, *Aristiguieta & Medina 3599* (NY, VEN); Páramo de la Cristalina, *Jahn 12* (US, VEN); Dtto. Carache, above La Laguneta, Páramo de El Turmal, near Edo. Lara, *Ruiz-Terán & Lopez-Figueras 906* (MERF, MO). MÉRIDA: Páramo de Timotes, *Alston 6622* (BM); Sierra Nevada, near Laguna Coromoto, *Barclay & Juajibioy 9985* (RSA); Páramo de Santo Domingo, Cascada La Victoria, *Benítez de Rojas 1296* (MY); 5 km above El Rincón de La Venta, Timotes-El Aguila, *Berry 3136* (MO, VEN); 36–38 km from El Aguila to Piñango, *Berry 3137* (MO, VEN), *Luteyn et al. 6193* (NY); 24 km above Timotes on road to El Aguila, *Berry 3278* (MO—2 sheets, VEN); Mesa de Los Pinos, above La Mucuy, *Berry 3443* (MO, VEN), *3444* (MO), *3446-B* (MO—2 sheets), *3447* (MO); along artificial lake above Hotel Los Frailes, 12.5 km below Apartaderos, *Berry 3465* (MO, VEN), *3598* (MO); entrance to Hotel Los Frailes, *Berry 3652* (MO); 73 km NE of Mérida, road to Barinas, *Breteler 3354* (NY, S, U, US); between Mucubají and Sto. Domingo, *de Bruijn 939* (MER, MO, VEN), *Dennis 2120* (K); 4 km from Laguna Mucubají towards Sto. Domingo near artificial lake, *Foldats 2469* (VEN—2 sheets); Chachopo, *Funck & Schlim 798* (BM, CGE, F, G-DC, MPU, OXF, P); Páramo de Timotes, *Jahn 508* (GH, US); Timotes, *Karsten s.n.* (W); Páramo de los Conejos, *Lasser 511* (US, VEN); San Martín, 10 km S of San Rafael de Mucuchíes, *Ruiz-Terán 992* (MER—2 sheets); near Minigú, 10–15 km S of San Rafael de Mucuchíes, *Ruiz-Terán 997* (MER, MO), *7208* (MO); between Laguna de Coromoto and Qda. El Oso, *Ruiz-Terán & López-Palacios 1663* (MERF, MO); Laguna Brava, between Río Los Granates and Loma La Paja, Páramo Los Granates, 15 km E of Sierra Nevada de Sto. Domingo, *Ruiz-Terán 6281* (MERF, MO); Cañada Cerrada, between Chachopo and El Aguila, *Ruiz-Terán & Dugarte 12947* (MERF, MO); Las Tapias, from Apartaderos to Barinas, *Ruiz-Terán 13438* (MERF); near Laguna de Coromoto, *Schulz et al. 326* (MER, U, VEN); above Chachopo, *Steyermark 56751* (F, NY, VEN); La Aguada, *Vareschi s.n.* (MER).

Fuchsia membranacea is an opposite-leaved member of sect. *Hemsleyella* that inhabits upper cloud forest and penetrates into subpáramo vegetation. In both areas, it can be found as a liana, epiphyte or terrestrial shrub on rocks or in humus. In habit and in many vegetative characters, it strongly resembles *F. tillettiana,* which has a similar distribution in Venezuela, but these species differ in habit and several floral traits. *Fuchsia membranacea* occurs in higher cloud forest, including the subpáramo, between 2,750 and 3,400 m, whereas *F. tillettiana* grows in cloud forest between 1,600 and 2,650 m. In *F. membranacea,* the filaments are shorter and greenish, the sepals are non-reflexed and dull pink to green, and the flowers are glabrous and axillary or grouped at the branch tips, but not subracemosely, as in *F. tillettiana.* Because of the absence of morphologically or ecologically inter-

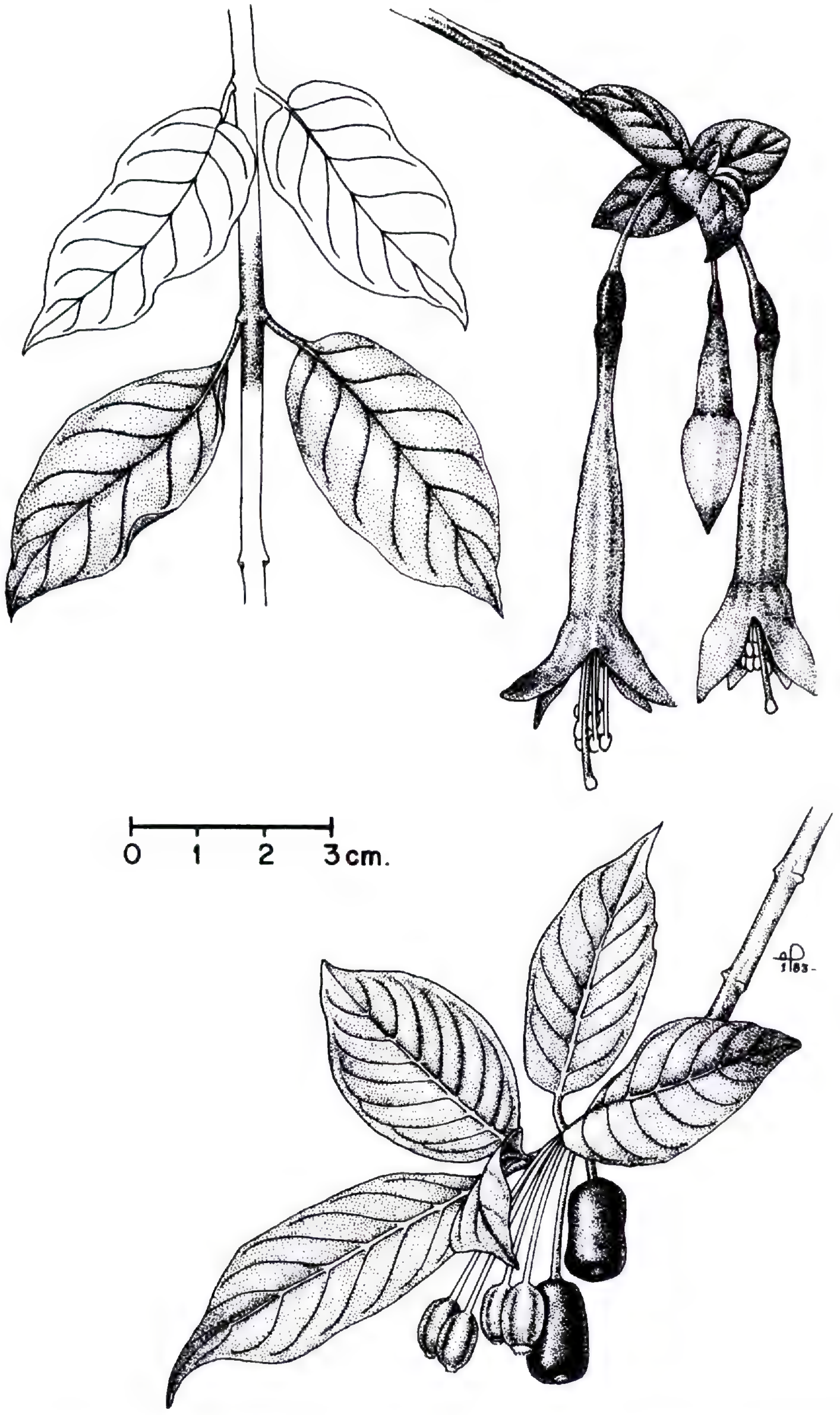

FIGURE 17. *Fuchsia membranacea*, flowering branch from *Berry 3465*, Edo. Mérida, Venezuela; leaves and fruiting branch from *Berry 3136*, Edo. Mérida, Venezuela.

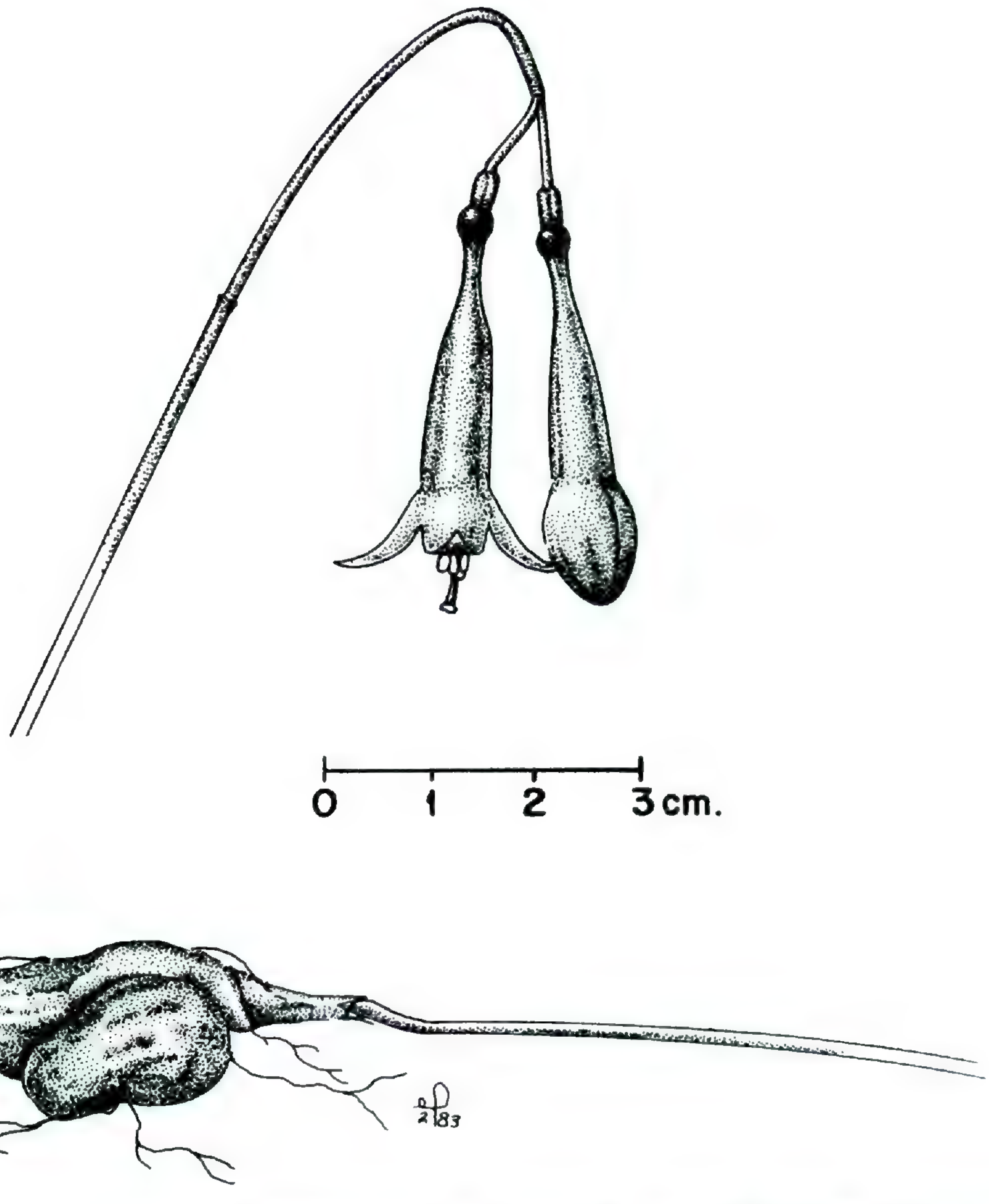

FIGURE 18. *Fuchsia nana,* flowering branch and tubers, from *Berry & Berry 2581,* Dept. Cochabamba, Bolivia.

mediate plants, both taxa are recognized as distinct species.

10. Fuchsia nana P. Berry, sp. nov. TYPE: Bolivia. Dept. Cochabamba: Incachaca Pass, on rocks and amongst overhanging roots on a bank above the road, 3,500 m, Aug. 1950, *Brooke 6920* (holotype, BM; isotypes, F, G-DEL, NY, U). Figure 18.

Frutex nanus epiphyticus saxatilisve; caules erecti vel repentes 3–10 dm longi, stolonibus 2–8 dm longis et tuberibus numerosis lateralibus ellipsoidalibus cupreis. Folia alterna saepe hysterantha, membranacea, ovato-lanceolata, apice acuminata, basi rotundata. Flores pauci axillaresque ad apicem ramorum juniorum, pedicellis 10–14(–19) mm longis. Tubi florales infundibuliformes, 21–29(–31) mm longi, basi ca. 3 mm lati bulbosique, superne dilatati summo 7–8 mm lati. Sepala lanceolato-ovata, 12–14(–16) mm longa, 5–8 mm lata, basi connata 2–3 mm.

Erect to creeping subshrubs 3–10 dm tall in rocks, or epiphytic in trees, with stoloniferous stems 2–8 dm long and numerous ellipsoid, copper-colored tubers lateral to the stem. Branchlets glabrous to loosely pilose, terete, 1.5–3 mm thick, reddish to copper; older stems 2.5–4 mm thick, with freely exfoliating bark. Leaves alternate, usually absent when flowering, membranous, (narrowly) lance-ovate, 20–35 mm long, 10–20 mm wide, apex acuminate, base rounded, glabrous above, usually pilose along the nerves below and sometimes purple-tinged; margin remotely denticulate, secondary veins 4–5 on either side of the midvein. Petioles 7–11 mm long. Stipules filiform, 1.5–2 mm long, deciduous. Flowers few and axillary near the tips of young shoots. Pedicels slender, glabrous, 10–14(–19) mm long. Ovary cylindrical to ellipsoid, 7–7.5 mm long, 2–3(–4) mm wide, lustrous cherry red, glabrous to pilose. Floral tube funnelform, 21–29(–31) mm long, ca. 3 mm wide and more or less bulbous

at the base, constricted above the base to ca. 2 mm wide, then widened above until 7–8 mm wide at the mouth, glabrous to sparsely pilose outside, pilose inside in lower ½. Sepals lance-ovate, 12–14(–16) mm long, 5–7(–8) mm wide, apex acute to obtuse, connate for 2–3 mm at the base, divergent at anthesis. Tube and sepals bright red-pink, with a dark purple ring usually present around the mouth of the tube. Nectary 2–3 mm high. Filaments red, the antesepalous ones 8–10 mm long, the antepetalous ones 6–8 mm long; anthers ellipsoid, cream, 2–2.5 mm long, 1–2 mm wide. Style red-pink, densely retrorse villous in lower ½; stigma green, globose, ca. 1.5 mm long and wide, exserted 5–10 mm beyond the anthers. Young berry ellipsoid, 11 mm long, 6 mm wide.

Distribution. Endemic to upper cloud forest in Dept. Cochabamba, Bolivia, (2,000–)3,000–3,700 m. Flowering principally in the dry season, from (April to) July to November. Figure 10.

Specimens examined. BOLIVIA. COCHABAMBA: Km 100 of Cochabamba-Villa Tunari road, *Badcock 313* (K); below and N of Lago de Corani along road to Chapare, *Berry & Berry 2581* (MO); Incachaca District, *Brooke 3738* (BM—mixed collection, F, NY); Toralapa, way to Yungas de Vandida, *Cárdenas 3753* (POM); Plumerito, 18 km from Colomi to Tablas, *Cárdenas 4090* (RSA); Cumbre de San Mateo-Vallegrande, *Cárdenas 4091* (RSA), *4092* (RSA); Km 28 between Colomi and truck terminal on way to Tablas, *Cárdenas s.n.* (RSA).

Fuchsia nana is readily recognized by the small size of the plant and its lustrous red-pink flowers with tubes just 2–3 cm long. It is a highly seasonal and almost exclusively epiphytic species, flowering when leafless and bearing many small tubers. Whereas the other members of sect. *Hemsleyella* in Dept. Cochabamba grow at lower elevations, *F. nana* inhabits the upper limit of the cloud forest. Both the high altitudinal range and the characters mentioned above would appear to relate *F. nana* most closely to *F. apetala.*

11. Fuchsia pilaloensis P. Berry, sp. nov. TYPE: Ecuador. Prov. Cotopaxi: around Pilaló, 79°02′W, 0°57′S, 2,400 m, 9 July 1968, *Holm-Nielsen & Jeppesen 1547* (holotype, AAU; isotypes, DS, S). Figure 19.

Frutex terrestris erectus usque 1 m altus vel epiphyticus, ramis pendulis elongatis, tuberibus interdum adsunt. Folia plerumque alterna aliquando opposita, membranacea, anguste ovata, apice acuminata, basi acuta vel rotundata, 40–122 mm longa, 25–54 mm lata, petiolis 15–38 mm longis. Flores pauci vel numerosi in ramulis axillaribus vel ad apicem ramorum aggregati, pedicellis 15–22 mm longis. Tubi florales anguste infundibuliformes, 44–53 mm longi, basi 3–4.5 mm lati bulbosique inde 2–3 mm lati constricti, superne gradatim dilatati summo 6–10 mm lati. Sepala anguste ovata, 13–20 mm longa, 7–8 mm lata, apice acuta, basi 4–7 mm connata, limbis sub anthesi valde patentibus.

Terrestrial shrubs 0.5–1 m tall or lianas or epiphytes with long, hanging branches to 8 m high in trees; tubers sometimes present or else thickened stems 10–20 mm diam. Branchlets terete, dull purple-green, densely pilulose, 2–4 mm thick; older branches reddish purple, freely exfoliating. Leaves usually alternate, occasionally opposite or subopposite, membranous, narrowly ovate, 40–120 mm long, 25–54 m wide, often unequal on either side of the margin, apex acuminate, base acute to rounded, subglabrous to scattered pilose above, pilose below along nerves and margins; margin subentire to denticulate, secondary veins 6–9 on either side of the midvein. Petioles pubescent, 15–38 mm long. Stipules filiform, ca. 2 mm long, 0.2–0.4 mm wide, deciduous. Flowers few to many, grouped towards the tip of branches or axillary branchlets, sometimes subtended by reduced leaves. Pedicels pilose, usually pink, 15–22 mm long. Ovary cylindrical, 5–7 mm long, ca. 2 mm wide, dull purple, pubescent. Floral tube narrowly funnelform, 44–53 mm long, 3–4.5 mm wide and bulbous at the base, then narrowed to 2–3 mm wide in lower ⅓ and gradually widened above until 6–10 mm wide at the rim, densely pilose outside, pilose inside in lower ⅓. Sepals narrowly ovate, 13–20 mm long, 7–8 mm wide, apex acute, connate at base for 4–7 mm, lobes strongly spreading at anthesis. Tube pale pink; sepals whitish to pale pink, sometimes greenish in bud. Nectary green-purple, lustrous, 3–4 mm high. Filaments dull green, the antesepalous ones 12–15 mm long, the antepetalous ones 7–9 mm long; anthers oblong, yellow, 3–4 mm long, 2.5–3 mm wide. Style pale pink, densely retrorse villous in lower ½, stigma globose, green, ca. 2 mm long, 2–2.5 mm wide, slightly 4-cleft at the apex. Berry 4-angled before maturity, oblong, verrucose, purplish; mature berry not seen.

Distribution. Known only from cloud forest above Pilaló, Prov. Cotopaxi, Ecuador, 2,400–3,150 m. Known to flower in June and July. Figure 15.

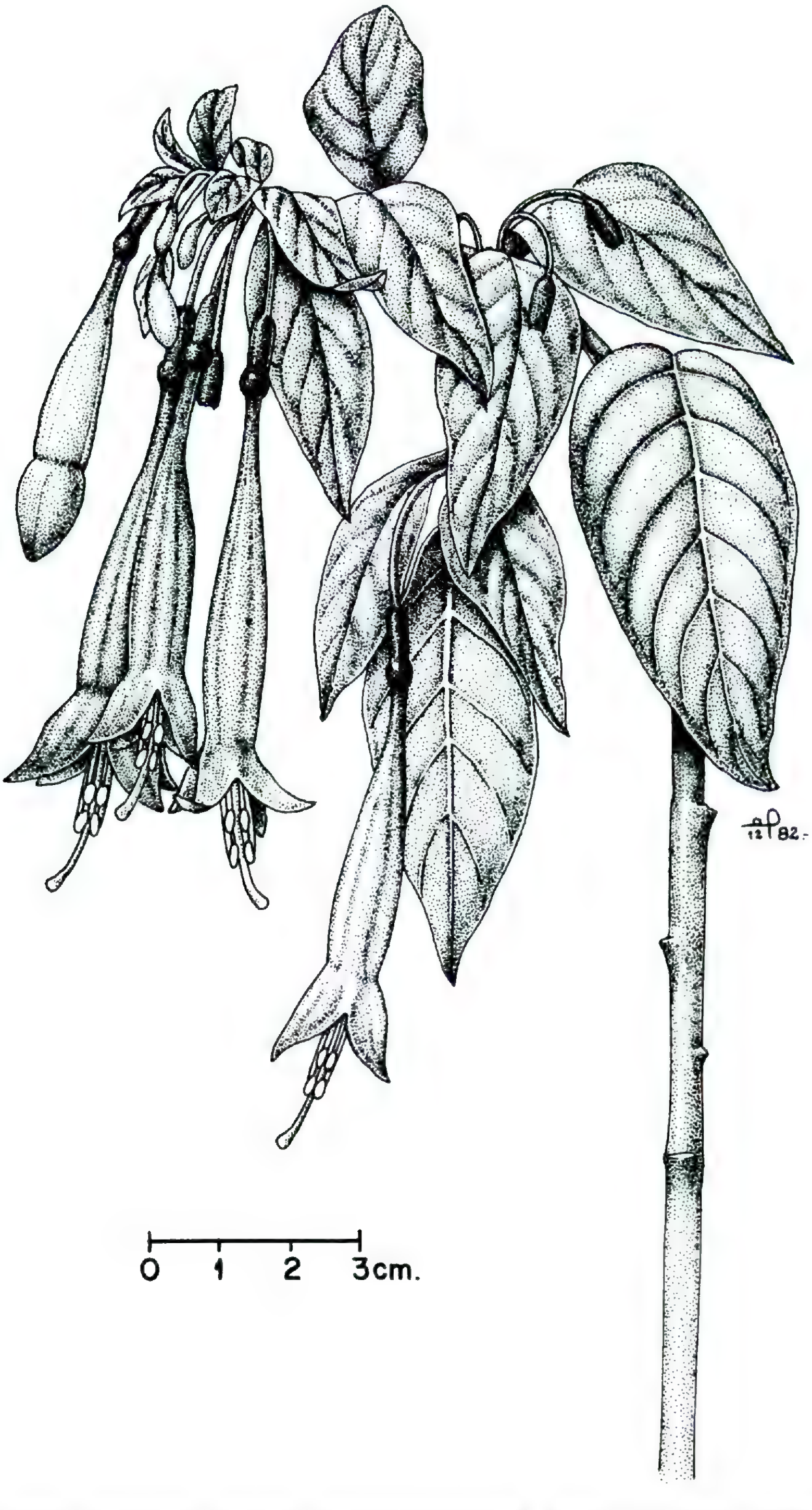

FIGURE 19. *Fuchsia pilaloensis,* flowering branch from *Berry & Berry 2551,* Prov. Cotopaxi, Ecuador.

Specimens examined. ECUADOR. COTOPAXI: 10 km above Pilaló on Quevedo-Latacunga road, 3,150 m, *Berry & Berry 2548* (MO, Q); 5 km above Pilaló, 2,760 m, *Berry & Berry 2551* (MO); 7 km above Pilaló, *Albert de Escobar & Escobar-Uribe 1479* (MO, TEX). CULTIVATED: Berkeley, California, *Univ. Calif. Botanical Garden Accession N° 58.782-1,* originally collected by C. K. Horich in Prov. Cotopaxi, Ecuador, between Pilaló and Macuchí, *Hutchison,* 1961 (RSA, UC), 1965 (RSA).

FIGURE 20. *Fuchsia salicifolia*, flowering branch from *Vargas 3486*, Prov. La Convención, Dept. Cuzco, Peru.

This species is restricted to an area of western Ecuador where no other species of sect. *Hemsleyella* is known, but where several species of sect. *Fuchsia* occur (Berry, 1982). *Fuchsia pilaloensis* is characterized by its light pink, narrow-tubed flowers, with pale sepals and narrowly ovate, mostly alternate leaves. In the same local area, this species has been found both as a small terrestrial shrub with leaves as well as a profusely flowering climber or epiphyte; no tubers were detected in either case.

12. Fuchsia salicifolia Hemsley, J. Bot. 14: 70. 1876. Munz, Proc. Calif. Acad. Sci., Ser. 4, 25: 78. 1943. TYPE: Bolivia. Dept. La Paz: Prov. Nor Yungas, Sandillani, 7,000–8,000 ft., Apr. 1866, *Pearce* (holotype, K). Figure 20.

Fuchsia tuberosa Krause, Repert. Spec. Nov. Regni Veg. 1(11): 170. 1905. *Fuchsia tuberosa* Krause var. *typica* Munz, Proc. Calif. Acad. Sci., Ser. 4, 25: 76, pl. 12, fig. 66. 1943. TYPE: Peru. Dept. Puno: Prov. Sandia, between Sandia and Cuyocuyo, in rocks, 2,700–2,800 m, *Weberbauer 875* (holotype, B, destroyed in World War II, photograph at F; isotype, G-DC).

Epiphytic shrubs on tree trunks, occasionally growing in rocks. Stems sometimes stoloniferous, with globose-ellipsoid tubers 2–3 cm diam., the stems often growing down tree trunks for several meters under moss. Branchlets terete, 2–4 mm thick, smooth reddish, subglabrous to lightly pubescent; older stems 5–15 mm thick with freely exfoliating bark, often 1–3 m long and hanging when epiphytic. Leaves alternate, firmly membranous, (narrowly) lanceolate, 60–135(–160) mm long, 18–37(–40) mm wide, apex generally long acuminate, base acute to rounded and often unequal, pale green and subglabrous above, light green to purplish and subglabrous below; margin remotely denticulate, secondary veins 7–9 on either side of the midvein. Petioles 5–20(–30) mm long. Stipules filiform, 1.5–2 mm long, ca. 0.3 mm wide, deciduous. Flowers generally few, axillary or clustered near branch tips. Pedicels slightly pubescent, 12–30 mm long. Ovary (narrowly) cylindrical, 8–11 mm long, ca.

2.5 mm wide, dull green, puberulent. Floral tube narrowly funnelform, 40–54(–60) mm long, 3–4(–5) mm wide and more or less bulbous at the base, then narrowed to 1.5–2(–2.5) mm in the lower ⅓ and gradually widened above until 7–10 mm wide at the rim, glabrous to puberulent outside, villous inside in lower ⅓. Sepals narrowly ovate, 23–30 mm long, 6–10 mm wide, apex acute to subacuminate, base connate for 2–4(–5) mm, spreading-divergent at anthesis, the distal portions sometimes curled back. Tube red-pink, sepals similar or paler, a dark purple ring usually present at the throat of the tube. Nectary 3–4.5 mm high. Filaments red to dark purple, the antesepalous ones 15–26 mm long, the antepetalous ones 12–20 mm long; anthers oblong, yellow, 2.5–3.5 mm long, 1–1.5 mm wide. Style pink, retrorse villous in lower ⅓; stigma globose to subclavate, dull green, ca. 2.5 mm long, 1.5–2 mm wide, exserted 6–12 mm beyond the anthers. Mature berry not seen.

Distribution. Southern Peru (Depts. Cuzco and Puno) and Dept. La Paz, Bolivia, in cloud forest, (2,000–)2,500–2,900 m. Flowers in the dry season, principally from July to October. Figure 10.

Specimens examined. PERU. CUZCO: La Convención, Huayopata, 10 km SW of Incatambo, *Peyton & King 1427* (MO); Pintobamba, El Dorado, La Convención, *Vargas 3486* (BH, CUZ, MO); Prov. Convención, Quellomayo to Lucumayo, *Vargas 4533* (CUZ, MO); Prov. Calca, Valle de Laco, Río Paucartambo, *Vargas 11106* (CUZ). PUNO: Prov. Carabaya, between Ayapata and Kahualluyoc, *Vargas 10765* (CUZ, W). BOLIVIA. LA PAZ: Prov. Nor Yungas, 10 km below Unduavi road to Coroico, *Berry & Berry 2578* (MO—2 sheets); Unduavi, *Rusby 1803* (NY); Prov. Nor Yungas, 6.7 km below Chuspipata on road to Yolosa, *Solomon 9683* (MO). WITHOUT LOCALITY: *Pearce 799* (K).

This species is best distinguished by its narrowly lanceolate, unequal leaves with long, acuminate tips and by its pink, narrowly funnelform floral tubes. Most specimens have leaves present together with flowers, but *Berry & Berry 2578* was almost leafless when collected.

Close examination of the isotype and the photograph of the destroyed holotype of *F. tuberosa* reveals that it is not specifically different from *F. salicifolia,* whereas Munz (1943), who did not have the opportunity to examine the type material, mistook *F. tuberosa* for what we now recognize as *F. chloroloba,* which also has tubers, but has orange-red and green flowers, a sharply constricted floral tube and entirely glabrous leaves and flowers.

13. Fuchsia tillettiana Munz, Aliso 7: 410. 1972. TYPE: Venezuela. Edo. Lara: Dtto. Jiménez, between Sanare and Laguna La Blanquita, 1,700 m, 24 Mar. 1970, *Tillett 703-35* (holotype, RSA-226553; isotypes, GH, MO, NY, US). Figure 21.

Fuchsia apetala sensu Munz, Proc. Calif. Acad. Sci., Ser. 4, 25: 80. 1943, pro parte.

Terrestrial shrubs 0.5–2 m tall, or growing in rocks, climbing up trees or epiphytic in trees to 10 m above ground; small, lateral tubers occasionally present in the soil on large plants. Branchlets puberulent, terete, 2–5 mm thick, red or copper-colored; older branches ascending on shrubs, flexuous and erect to drooping and to 10 m long on hanging bushes, the rooted portions often to 25 mm thick, with freely peeling, flaky bark. Leaves opposite or ternate, soft membranous, elliptic to narrowly ovate, (30–)55–100 mm long, (7–)16–50 mm wide, apex (sub-)acuminate, base rounded to acute, subglabrous to pruinous or puberulent above, subglabrous to puberulent and pale green below; margin subentire to serrulate, secondary veins 7–9 on either side of the midvein. Petioles puberulent, green or reddish, 6–12(–30) mm long. Stipules lance-triangular, 1–2 mm long, 1–1.5 mm wide. Flowers generally numerous at branch tips or subracemose; leaves often absent, or small bracts 15–30 mm long and 6–20 mm wide present when flowering. Pedicels red-purple, 25–50 mm long. Ovary cylindrical, more or less sulcate, 8–10 mm long, 2.5–3.5 mm wide, green to purplish, usually with glandular hairs. Floral tube funnelform, 36–46 mm long, 2–5 mm wide at the base, slightly narrowed in lower ⅓, then gradually widened until 7–9(–13) mm wide at the rim, glandular-pubescent outside, pilose inside in lower ⅓. Sepals lanceolate, 19–33 mm long, 4–6(–10) mm wide, apex acute, base connate for 2–3 mm, blunt-tipped in bud, strongly recurved at anthesis. Tube and sepals cerise or rose pink. Nectary glossy green, 3–4 mm high. Filaments pink to cerise or dark purple, the antesepalous ones 20–35 mm long, the antepetalous ones 15–28 mm long; anthers oblong, yellow, 4–5 mm long, 2.5–3 mm wide. Style pink, retrorse villous in lower ½–⅓, exserted 15–20 mm beyond the anthers; stigma green, clavate, ca. 3 mm long, 2–2.5 mm wide. Berry cylindrical, usually more or less narrowed at the apex, 18–21 mm long, 6–10 mm wide, puberulent, dull purple-green to lustrous bright red when ripe; seeds ca. 50 per fruit, light tan, 1.8–2 mm long,

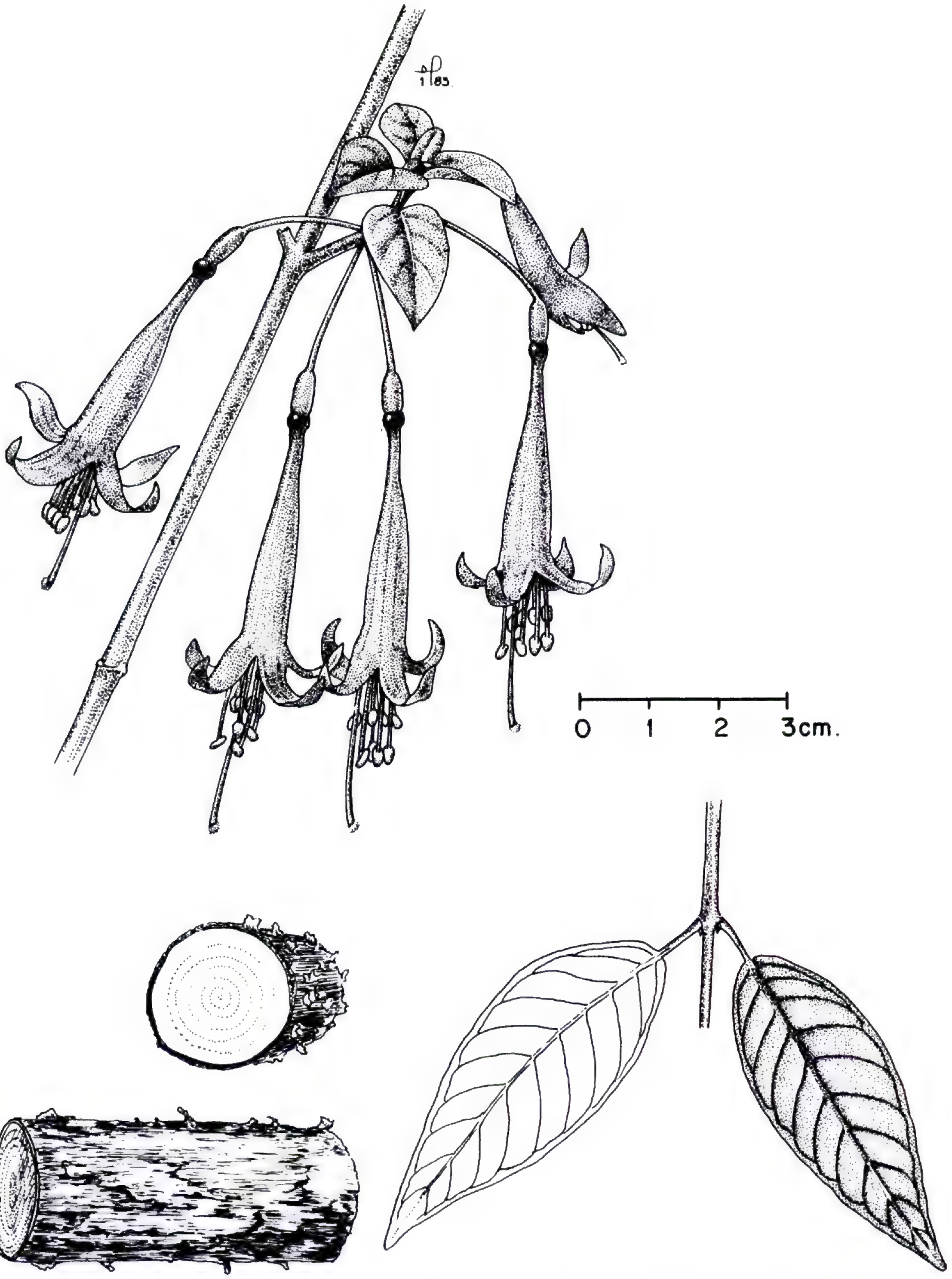

FIGURE 21. *Fuchsia tillettiana,* flowering branch from *Berry 3463,* Edo. Mérida, Venezuela; leaves and stem portion from *Berry 3265,* Edo. Lara, Venezuela.

1.3–1.6 mm wide. Gametic chromosome number, $n = 11$.

Distribution. Venezuelan Andes, cloud forest in Estados Lara, Trujillo, Mérida, and Táchira, 1,600–2,650 m; one doubtful collection from Colombia. Flowers mainly in the dry season when leafless, from January to April. Figure 15.

Specimens examined. VENEZUELA. LARA: Parque Nacional Yacambú, 13–17 km S of Sanare, *Berry 3265* (MO, VEN), *3267A* (MO), *3267B* (MO), *3467* (MO), *3469* (MO), *Dunsterville & Dunsterville,* 1969 (VEN), *Garófolo,* 1979 (MO), *Steyermark & Carreño 108848* (MO, VEN), *Tillett 711-26* (MER), *714-41* (MER). TRUJILLO: La Mesa de Esnujaque, *Box & Alayón 3710* (BM, VEN). MÉRIDA: 1.5 km above San José, road to Mucutuy, *Berry 3463* (MO, VEN), *4280* (MO, VEN); forest above La Veguilla, above Mucutuy, *Berry 3464* (MO, VEN), *4289* (MO, VEN); banks of Qda. La Campana, 4.2 km below La Mitisús on Barinas-Apartaderos road, *Berry 4314* (MO, VEN); between La India and El Morro, *Ijjasy-Madriz 451* (NY, VEN); Páramo de San José, *Jahn 969* (US, VEN); Páramo de Mucuchachí, *Jahn 981* (VEN); Páramo de Aricagua, *Jahn 1030* (US); Mucutaray, between San Isidro and Qda. Mucubají, more or less 15 km ESE of El Morro, *Ruiz-Terán & Lopez-Figueras 8603* (MERF, MO); Páramo de Pozo Negro, between San José and Beguilla, *Steyermark 56293* (F, NY, VEN). TACHIRA: Dtto. Cárdenas, 15 km E of Zumbador on road to Queniquea, *Berry 3303* (MO—2 sheets, VEN).

One of six opposite-leaved species in sect. *Hemsleyella, Fuchsia tillettiana* is most readily recognized by its glandular-pubescent floral tubes (best seen when fresh), strongly reflexed sepals, long filaments (20–35 mm long in the antesepalous whorl) and the cerise color in both the tube and the sepals. The flowers of *F. tillettiana* are grouped subracemosely at the branch tips, and anthesis usually occurs when the plant is leafless, although shade plants often bear leaves and flowers together. Tubers seldom occur on plants of *F. tillettiana,* but thick semisucculent stems seem to supplant the storage function of tubers in climbing and epiphytic plants. Woody, erect stems predominate when the species occurs as a terrestrial shrub, but when growing as a climber, plants produce long, flexuous stems that climb up to 10 m high in trees and then clamber or droop down over the adjacent vegetation.

Fuchsia tillettiana occupies approximately the same geographical range as *F. membranacea,* to which it is closely related; their main differences are discussed under *F. membranacea.*

A specimen of somewhat doubtful origin, *Dawe 896* (K, Colombia, in the páramos, tuberous), lacks leaves, but has pubescent flowers with narrow, though not evidently reflexed, sepals that agree most closely with *F. tillettiana.* The notation of the presence of tubers and of inhabiting páramos casts doubt, however, on it belonging to this species. More complete specimens with detailed locality information would be necessary to evaluate the proper placement of this collection.

14. Fuchsia tunariensis O. Kuntze, Revis. Gen. Pl. 3(2): 98. 1898. Munz, Proc. Calif. Acad. Sci., Ser. 4, 25: 79, pl. 13, fig. 68. 1943. TYPE: Bolivia. Dept. Cochabamba: Tunari Range, 3,000 m, Apr.–May 1892, *Kuntze* (holotype, NY, photograph at UC). The type collection is a very poor specimen with no flowers left, but the leaves agree well with the type description. Figure 22.

Fuchsia mattoana Krause, Bot. Jahrb. Syst. 37: 599. 1906. TYPE: Peru. Dept. Cuzco: Prov. Convención, road from Cuzco to Santa Ana, 3,400 m, June 1906, *Weberbauer 4976* (holotype, B, destroyed in World War II, photograph at F).

Shrub 0.8–1.5 m high, growing terrestrially in humus, on rocks, or epiphytically in trees, with cylindrical-ellipsoid tubers 1–3 cm thick and 8–15 cm long usually present. Young growth velutinous, pilulose or cinereous; branchlets terete, 2–4 mm thick, pilulose; older branches with freely exfoliating bark. Leaves opposite or less often alternate, membranous, broadly ovate to elliptic-ovate, 60–110(–115) mm long, 35–65 mm wide, apex (sub-)acuminate, base acute to cordate, subglabrous to pilulose above, scattered to densely pubescent below, especially along the nerves; margin remotely denticulate, secondary veins 6–9 on either side of midvein. Petioles pubescent, (10–)15–33 mm long. Stipules narrowly triangular, ca. 1.5 mm long, deciduous. Flowers generally few and axillary towards young branch tips. Pedicels finely pubescent, 15–30(–50) mm long. Ovary cylindrical, velutinous to pilulose, 9–11 mm long, 2.5–3 mm wide. Floral tube funnelform, (36–)44–56 mm long, 3.5–4.5 mm wide and more or less bulbous at the base, then slightly constricted to ca. 3 mm wide and widened gradually above until 6–10 mm wide at the rim, finely pubescent outside, villous inside for most of length. Sepals lanceolate to (narrowly) ovate, 17–25 mm long, 7–8(–9) mm wide, apex acute to acuminate, connate for 3–4 mm at the base, divergent at anthesis. Tube and sepals bright red-pink to light orange. Nectary 2.5–4 mm high.

FIGURE 22. *Fuchsia tunariensis*, flowering branch and leaves from *Berry 3051*, Dept. Ayacucho, Peru.

Filaments greenish, the antesepalous ones 14–20 mm long, the antepetalous ones 8–13 mm long; anthers oblong-ellipsoid, yellow, 3–3.5 mm long, ca. 2 mm wide. Style orange to pink, villous for most of length; stigma globose, green, 2–3 mm long, ca. 2 mm wide, exserted 6–20 mm beyond the stamens. Mature berry not seen. Gametic chromosome number, $n = 11$.

Distribution. Southern Peru and Bolivia. Rare in cloud forest from Dept. Ayacucho, Peru, to Dept. Cochabamba, Bolivia, 2,400–3,400 m. Flowers mostly at the end of the dry season, from September to November. Figure 10.

Specimens examined. PERU. AYACUCHO: 45 km E of Tambo on road to Ayna, *Berry 3051* (MO). CUZCO: W of Salcantay, *Hein,* 1946 (F); Prov. Convención, "El Dorado," *Vargas 3485* (BH, CUZ, MO); Prov. Paucartambo, Pillahuata, *Vargas 3673* (BH, CUZ, MO), *Vargas 16765* (CUZ), *West 7106* (GH, UC); Cosñipata, close to Paso El Aguila, *Vargas 17820* (CUZ); Prov. Calca, road to Chiriwayu, *Vargas 23049* (CUZ, MO). BOLIVIA. COCHABAMBA: Km 99 of Cochabamba-Villa Tunari road, *Badcock 312* (K); Choro, above Río Cocopata, 100 mi. NW of Cochabamba, *Brooke 6151* (BM, F), *6247* (BM); road to Incachaca, *Brooke 6809* (BM, F, NY); Km 103 of Cochabamba-Chapare road, *Cárdenas 5969* (DC, UC, US); Km 102 of Cochabamba-Aguirre-Todos Santos road, between Comercocha and Palmar, *Ugent & Ugent 5060* (DS, GH, K).

This species is best distinguished by its mostly opposite leaves and the soft, velutinous-cinereous pubescence on the leaves, flowers, and young shoots. The flowers are apparently uniformly colored, typically rose salmon to light orange, although the sepals may be slightly greenish at the apex. Many specimens bear leaves and flowers at the same time, and although the plants are characteristically tuberous, they can grow in a variety of situations—as epiphytes, or as terrestrial shrubs in rocks or in humus soil. Since this variety of habitats can give rise to considerable vegetative variation, and there are so few collections made of this species, with a considerable gap between the Bolivian and the Peruvian collection localities, more material is needed to determine if the plants from these two areas are really conspecific.

A single collection from Dept. Huánuco, Peru, is possibly a new species, most closely allied to *F. tunariensis*: *Meza 360* (MO, Peru, Dept. & Prov. Huánuco, Quebrada before Utao, 2,430 m, 4 Oct. 1965, shrub with pink flowers and greenish sepal tips) has opposite to ternate, ovate leaves, canescent-pilose pubescence, erect stems, pilose floral tubes 40 mm long (in bud) and sepals 12 mm long by 4 mm wide. The sepals of this plant, though still immature, are too small and contrast too strongly in color with the floral tube to be placed in *F. tunariensis,* but mature flowering specimens would be desirable before describing it as a new species of sect. *Hemsleyella.*

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COLLECTING AND PREPARING SPECIMENS OF ARACEAE

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The family Araceae is a conspicuous component of moist to very wet life zones in the tropics. Because of the frequently succulent and often large parts, the preparation of specimens is often difficult. A detailed discussion of all aspects to be considered in preparing descriptions of *Anthurium* (applicable as well to most other genera) was published for use by aroid workers (Croat & Bunting, 1979). This paper will deal only with those aspects which should be recorded when specimens are being prepared in the field. Since the family is well suited to cultivation, and since an increasingly higher percentage of the collections are also being collected and sent back alive, this paper will be divided into two parts: 1. herbarium specimens; 2. live collections.

HERBARIUM SPECIMENS AND FIELD NOTES

ECOLOGICAL ASPECTS OF ARACEAE

The diversity of habit types in Araceae is much greater than in most families (Simmonds, 1950; Madison, 1978) and special attention should be given to aspects of habit. Some members of the family, such as *Caladium, Chlorospatha, Dieffenbachia, Spathiphyllum,* and *Xanthosoma* are strictly terrestrial. Most temperate species such as *Arisaema,* and of course all tuberous members of subfamilies Lasioideae (e.g., *Dracontium, Amorphophallus,* etc.) and Aroideae, are also terrestrial. Quite a number of aroids are rooted aquatics in standing water, including *Orontium, Montrichardia, Urospatha,* and other genera. *Symplocarpus, Spathiphyllum,* and others occur in marshy habits or sometimes in standing water. Some *Spathiphyllum* and *Anthurium* species occur only on rocks along streams. Riparian species are particularly common in southwest Asia with genera such as *Holochlamys, Piptospatha,* and *Aridarum* frequenting such habitats. *Pistia* is a free-floating aquatic and *Jasarum* a rooted but wholly immersed aquatic. The largest percentages of aroid species are, however, either epipetric or epiphytic in one form or another. The types of epiphytism are diverse with some genera such as *Anthurium* and *Stenospermation* usually being true epiphytes while other genera like *Monstera, Syngonium,* and most *Philodendron* begin their life in the soil then eventually climb trees while becoming hemiepiphytes and at least in part often losing their connection with the ground to become true epiphytes. Some *Philodendron,* such as *P. wendlandii* Schott, have seeds which germinate only on tree branches and are thus true epiphytes. Still others such as *P. radiatum* Schott grow as true epiphytes until they eventually send roots to the ground at which time they must be classified as hemiepiphytes.

Many genera pass most of their adult lives slowly creeping up tree trunks. These are referred to as "appressed climbers" or "epiphytic creepers." However, depending on their situation, such plants in certain genera, notably *Monstera* and *Syngonium,* can revert again and again to juvenile forms owing to being dislodged from their host plant or merely because they have run out of space to climb. These reversions have been studied for *Monstera* (Madison, 1977) and especially for *Syngonium* (Ray, 1981; Croat, 1982). Leaf forms for juvenile plants, pre-adult plants (usually found down low on tree trunks), and adult plants are generally totally distinct and may even seem to be distinct species. If possible, one should collect juvenile and pre-adult forms.

The habit of *Philodendron* is particularly diverse with, for example, some species occurring only over the crowns of understory shrubs while others occur only on the lower portions of larger tree trunks and still others grow only high in the canopy where more light is available. To merely refer to all of these as epiphytes (the usual case) or epiphytic vines (in fact most are hemiepiphytic vines) does little justice to a complex array of life forms and habits. It is thus important when making aroid collections to make note of the habitat and habit of the collection. The habit of the collection is particularly important.

IMPORTANT MORPHOLOGICAL FEATURES

Since it is often not possible to collect the whole plant, certain morphological features are impor-

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TABLE 1. Synopsis of features to note for certain genera of Araceae.

Anthurium

Habit; internode length; petiole cross-sectional shape; disposition of inflorescence; color and disposition of spathe; color of spadix; color and shape of fruits.

Dieffenbachia

Height of plant; diameter, color and glossiness (matte or glossy) of stem; cross-sectional shape, color and markings of petioles; color and markings of leaves; shape of upper midrib.

Homalomena

Scent of cut parts; coloration and variegation of leaves.

Monstera

Habit; length, coloration, and markings of internodes; collect juvenile and pre-adult leaves if possible; color of spathe and spadix.

Philodendron

Habit; internode length and color; cataphylls deciduous or persistent, kind and degree of ribbing; cross-sectional shape of petiole; shape of midrib on upper surface; prominence of minor veins on lower surface; color of sap; number of inflorescences per axil; color of spathe (inside and outside).

Rhodospatha

Habit; internode length; color of spathe and spadix.

Spathiphyllum

Habitat; degree of clustering; spathe and spadix color; color of tepals; color and degree of protrudence of pistils.

Syngonium

Habit; internode length; collect juvenile and pre-adult leaves if possible; number of inflorescences per axil.

Xanthosoma

Spathe tube color (inside and outside); color of female spadix.

tant to note. These are summarized for certain important genera in Table 1.

Stem. Numerous taxonomic characteristics are exhibited by the stem. Obviously in climbing genera, such as *Monstera, Philodendron,* and *Syngonium,* the internode length can be important. If it is not possible to collect the stem either because of its size or because the stem is being used as a live specimen, one should make note of the length and width of the internodes. In most climbing genera even one or two internodes included with the specimen yields considerable information because many species have unique colors on drying or are fissured in characteristic manners. The stems of *Philodendron* and other scandent genera may be variously flattened on one side or variously sulcate providing useful taxonomic characteristics. Though most of the figures in this paper lack stems because the stems were taken for cultivation, it is always best to include the stem if it is not to be used.

FIGURE 1. Stem with several nodes, cataphyll and both surfaces of blade.

On large stems it is best to cut off a small portion of the apex of the stem, then split the stem longitudinally (or even remove all but a thin portion of the outer part of the stem so that the uppermost cataphyll is still intact). If possible and the size of the petiole does not prohibit it, the uppermost petiole should be left with the stem tip (Fig. 1).

Cataphylls. Philodendron, a large and taxonomically complex genus, has cataphylls that provide several important taxonomic characteristics. Cataphylls are bract-like structures at least partially encircling the stem, at or near the apex, and subtending each new leaf for its protection as it emerges. They may be present or absent (in

FIGURE 2. One-half of large blade with midrib and petiole, folded to show base and apex.

FIGURE 3. Large blade with apex folded back (slightly to one side to expose primary lateral veins and the sinus).

the case of some entire sections of the genus, e.g., sect. *Pteromischum,* where protection of the new leaf is accomplished by a sheathing petiole of an earlier leaf) and may be variously colored. Cataphylls may also be unribbed, 1-ribbed, or 2-ribbed and at the same time they may be deciduous or variously persistent (either remaining intact or more usually weathering to a mass of persistent fibers which envelop the stem). At least the apical portion of the stem is thus essential for an adequate specimen.

Petioles. Petiole cross-sectional shape on many genera including both *Philodendron* and *Anthurium* is one of the most valuable taxonomic characteristics and should be noted. Because this feature is so variable and because a typical shape has been described so differently by different collectors, an illustration of the various petiole shapes along with descriptive terminology is included (Fig. 9).

Blades. When blades are small, it is best not to fold the blade but to prepare the specimen with the lower surface up (Fig. 1). The lower surface, because of the generally more pronounced venation, provides more characters. On a larger blade it is best to slice off one-half of the blade leaving the midrib and petiole with the half which is to be saved (blades of Araceae are generally bilaterally symmetrical but where not, this technique should be replaced by making one or more sections of the blade perpendicular to the midrib). The half leaf can then be folded accordian style to fit a standard sized newspaper for specimen preparation (Fig. 2). It is important to start at the base of the blade with the lower surface facing upward, then fold the apical lobe over so that it is directed slightly to one side so the midrib and the sinus (space between the posterior lobes) is still visible (Fig. 3). When the blade is particularly long, two or more folds can be made, but particularly large blades should be cut in half perpendicular to the midrib and mounted on two sheets (Figs. 4, 5). When blades are wide and the basal portion will not fit on a standard sized herbarium sheet, the lower portion can be placed on the sheet sideways (Fig. 6) with the remainder folded on a second sheet. If a speci-

FIGURES 4, 5. Blade cut perpendicular to midrib and placed on two sheets.

men is of moderate size, the petiole, stem, and inflorescence can be accommodated on the same sheet. After folding the blade (usually only one can be accommodated) in the manner described above, the petiole, section of stem apex, and the inflorescence (usually in one of uppermost axils) can be folded over the leaf. This method can at least be used for initial field drying, then if the value of the collection warrants it, the collection can later be cut along the fold lines and mounted on separate sheets.

Inflorescence. Because of the unusual nature of flower morphology, some discussion is warranted (see Croat & Bunting, 1979, for a more detailed treatment).

Araceae flowers are invariably quite small and are borne in congested spikes (or spadices) which are, at least initially, always enveloped by a conspicuous spathe. Flowers may be unisexual (in which case plants are usually monoecious) or bisexual. When they are unisexual, the female (pistillate) flowers are always borne on the lower part of the spadix and mature first (aroids are all believed to be protogynous). The male (staminate) flowers are borne on the usually much longer upper part of the spadix. The lower part of the staminate spadix often bears a small section of sterile male flowers. A few genera in the old world, e.g., *Alocasia* and *Amorphophallus,* bear an elongated, often conspicuous, appendage at the apex above the male spadix. In the case of unisexual flowers, the respective sections of the spadix may be of different colors and these should be noted. Bisexual flowers are borne in uniform spadices and are usually of uniform color though the tepals may be a different color than the pistils. Color changes may also occur after anthesis and sometimes it is possible to note these by observing several inflorescences on a plant or several plants in a population.

The spathe color is taxonomically important and should be noted. Like the spadix, color changes often occur after anthesis and if so, these should be noted. Species with convolute spathes (such as *Philodendron*) may have the spathe colored differently on the inner surface than on the outer surface. These important differences should be noted. Since many genera may have massive inflorescences or infructescences, it is often wise to dissect the spadix longitudinally for better

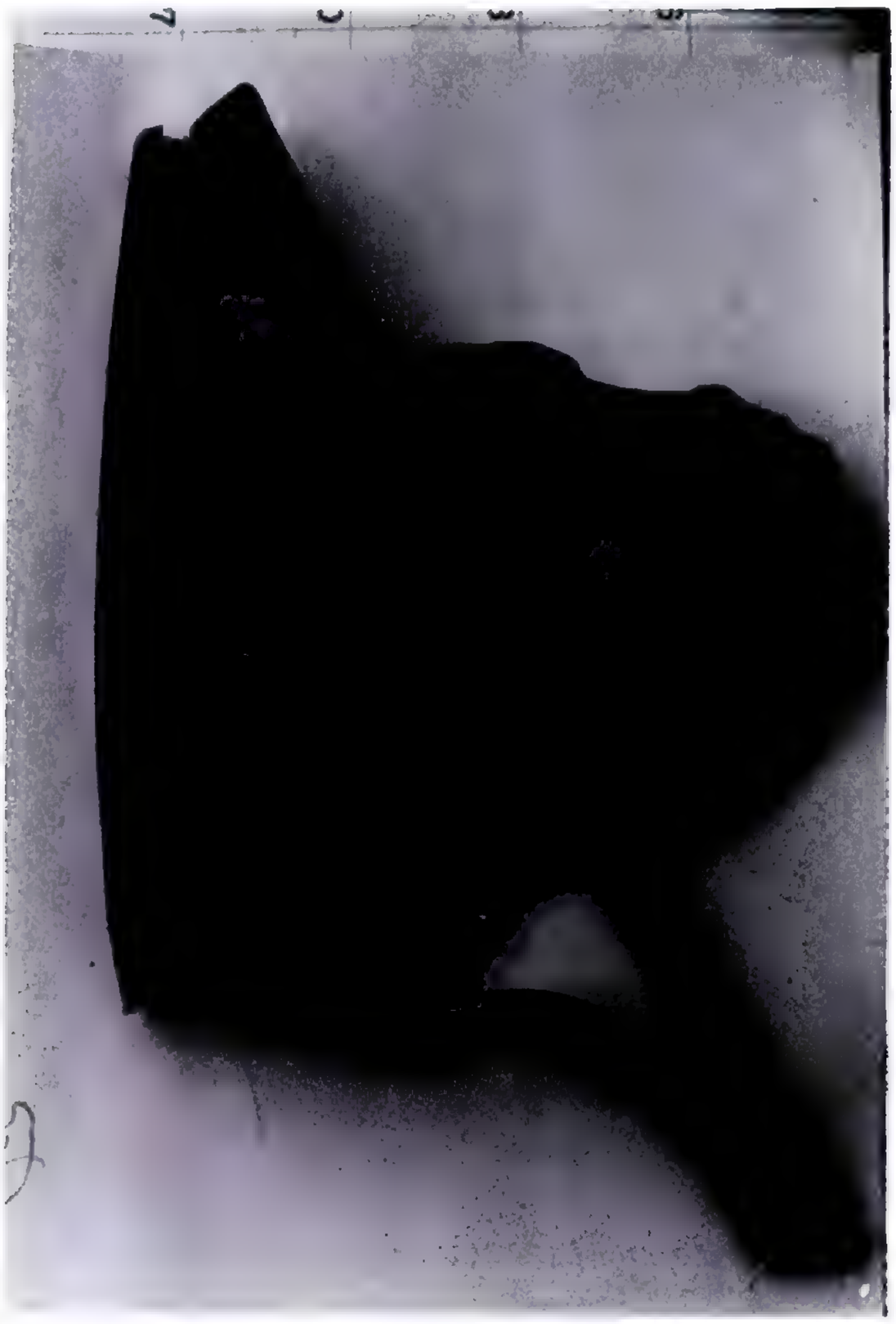

FIGURE 6. Lower portion of blade placed sideways on sheet to accommodate broad blade (upper half of blade dried in a separate sheet).

FIGURE 7. Spathe removed by cutting the base near peduncle attachment and by pulling the two sections apart.

drying. Genera with convolute, closed spathes pose special problems since the spadix enclosed in them exhibits important characters which must be exposed. Ideally it is best to leave one inflorescence intact (if it can be dried) and dissect another to expose the spadix. One method is to remove the spathe completely by cutting around the spathe just above its attachment with the peduncle (Fig. 7). Another method is to cut a large window in the spathe at the base to expose the pistillate portion and at least the base of the staminate pattern (Fig. 8). It is important to make note of any differences in coloration of the male and female portions, because in many cases they are not the same.

Fruit. Color and shape of fruits are taxonomically important and should be reported accurately since even where live material exists, it is often not possible to successfully pollinate the plant and thus study the fruits. Fruits usually are solid colored but are often bicolorous with the lower portions usually paler. Recording the shape of the berries is important because drying greatly distorts them.

PREPARATION AND SHIPMENT OF LIVING MATERIAL

Most Araceae are either epiphytic or have short internodes and are easily shipped live. Generally the most difficult to ship live are slender stemmed vines especially those with long internodes such as *Heteropsis* or *Philodendron* (sect. *Pteromischum*). Generally a live specimen should consist of at least three nodes (preferably more). The most successfully transplanted cuttings are usually about 15–20 cm long (6–8 in.). Old cataphylls, as well as all leaves and roots, should be removed as they usually perish during shipment. Generally dirt and debris can be removed by wiping the stems with your hands or a rag and a knife can be used to scrape off more difficult to remove dirt. Washing with a brush in clean moving water is good but all excess water must be blotted off or stems must be allowed to air dry before packaging to prevent mold. Individual cuttings should be tagged first then wrapped in small pieces of newspaper. The cuttings should be gathered into plastic bags, tightly sealed, and

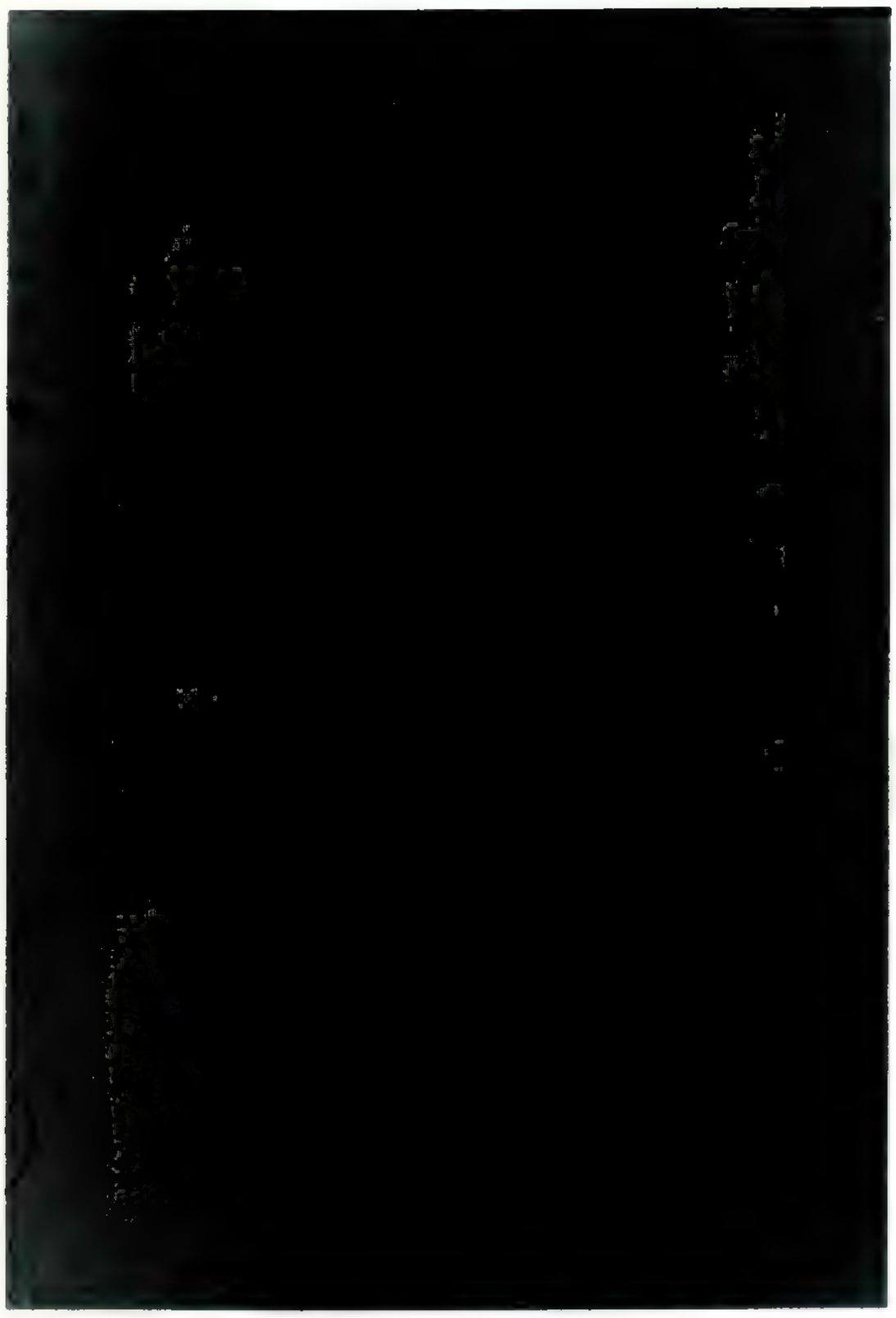

FIGURE 8. Spathe cut to expose portion of spadix (including lower pistillate portion, sterile staminate flowers and the lower half of the staminate spadix).

kept in a shady, preferably cool, place until shipped.

Aluminum tags that can be written on with a ballpoint pen are excellent and are designed to wrap around the stem. Masking tape wrapped around the stem also persists well but should be marked with an indelible marker. Paper tags often fall off before they arrive. Never attempt to ship stems with the tag attached to a petiole or around the tip of the stem as petioles are soon deciduous and tags often fall off of the generally pointed tip of the plant. For additional information concerning the availability of different types of tags, see Croat (1984).

Generally, the simplest and cheapest way to send back live material is to collect fruits and prepare the seeds for shipment. Aroid fruits are invariably fleshy and the seeds must be removed from the berry to meet importation requirements. This is easily done by careful maceration in a bowl. If the resulting material is flushed with water, the pulpy mesocarp usually floats to the surface and can be removed by decantation. The seeds are then wrapped in a small piece of dry

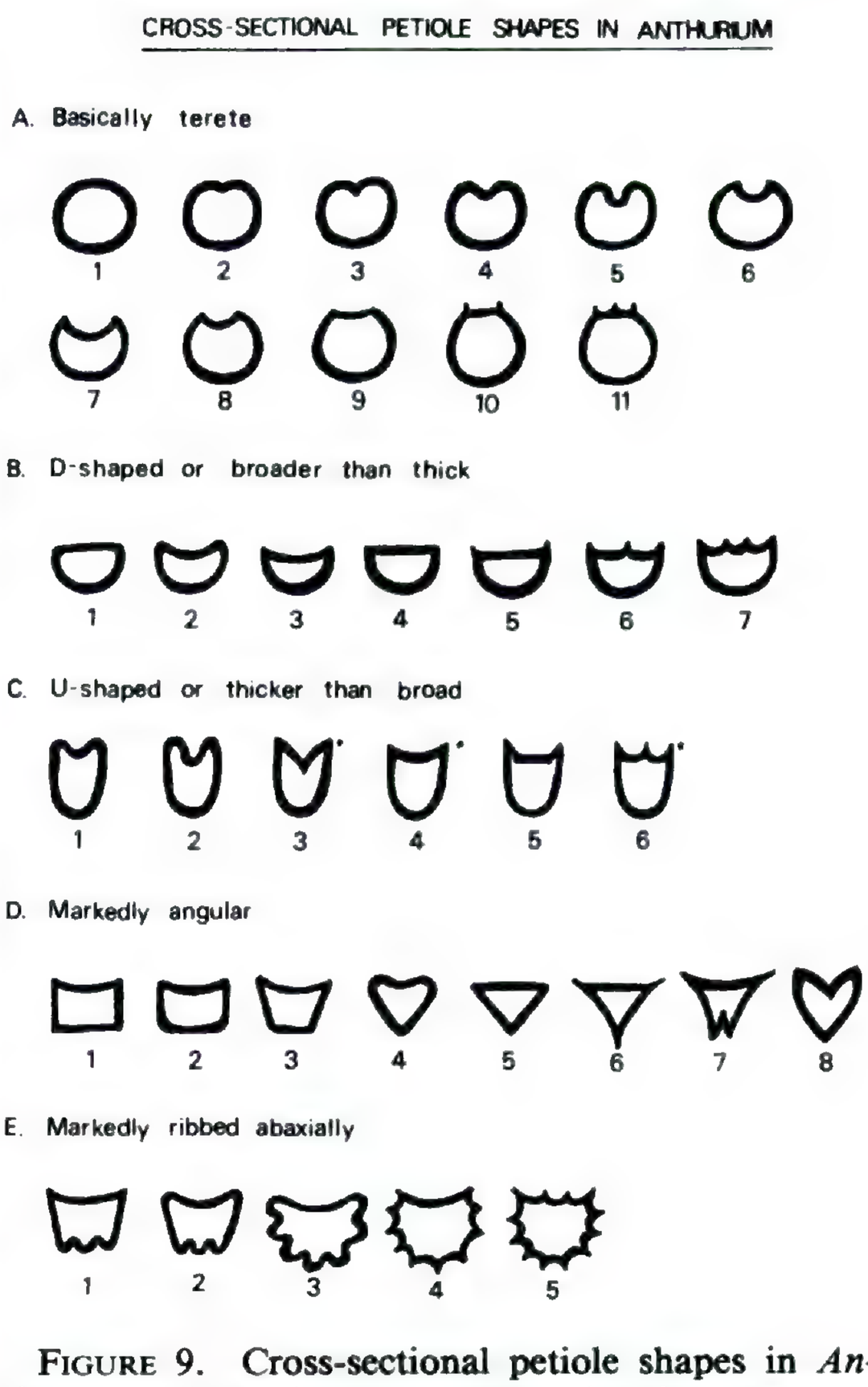

FIGURE 9. Cross-sectional petiole shapes in *Anthurium*.—A. Basically terete: ranging from esulcate (1), to shallowly and acutely sulcate (2, 3), to obtusely and broadly sulcate (4), to narrowly and obtusely sulcate (5), to narrowly and acutely sulcate (6), broadly and acutely sulcate (7), shallowly sulcate (8), flat adaxially (9), flat adaxially with marginal ribs (10), to flat adaxially with marginal and medial ribs (11).—B. D-shaped or broader than thick: ranging from flat adaxially with obtuse margins (1), to broadly sulcate with obtuse margins (2), broadly sulcate with acute margins (3), sharply D-shaped (4), flat adaxially with erect margins (5), and flat adaxially with erect margins with one or more medial ribs (6, 7).—C. U-shaped or thicker than broad: ranging from broadly and obtusely sulcate (1), to narrowly and obtusely sulcate (2), narrowly and acutely sulcate with acute margins* (3), shallowly and acutely sulcate* (4), sulcate with acute margins (5), sulcate with sharp margins and a medial rib* (6).—D. Markedly angular: ranging from quadrangular with acute angles (1), to quadrangular with obtuse angles (2), trapezoidal (3), obtusely triangular (4), acutely triangular (5), acutely triangular with two marginal ribs (6), basically triangular with two abaxial ribs (7), obtusely triangular, narrowly and sharply sulcate with convex sides (8).—E. Markedly ribbed abaxially: ranging from trapezoidal or quadrangular, sharply and broadly sulcate adaxially, 3-ribbed abaxially (1), to obtusely and broadly sulcate adaxially, 3-ribbed abaxially (2), broadly and obtusely sulcate adaxially, 5-ribbed abaxially (3), broadly and sharply sulcate adaxially, narrowly and sharply ribbed around the remaining circumference (4), or with one or more ribs on the sulcus (5). *Not yet observed but to be expected.

newspaper or toweling, marked, and placed in a *sealed* plastic bag before being mailed. If there is danger they will be smashed, extra toweling or newspaper could be placed on the outside of the plastic bag or a padded envelope could be used.

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DIMORPHIC INCOMPATIBILITY IN *TURNERA HERMANNIOIDES* CAMB. (TURNERACEAE)[1]

SPENCER C. H. BARRETT AND JOEL S. SHORE[2]

ABSTRACT

Turnera hermannioides (Turneraceae) is a distylous, diploid, perennial restricted to open, sandy sites in northeastern Brazil. Four populations sampled in Sergipé contained equal proportions of long- and short-styled plants. The style and stamen dimorphism in floral morphs is associated with differences in pollen size and pollen production. In contrast, flower size, ovule number, and seed fertility of the morphs are not significantly different. A controlled pollination program demonstrated that individuals of *T. hermannioides* possess a self- and intra-morph incompatibility system. The only pollinations resulting in significant seed production were between the floral morphs. Populations of *T. hermannioides* grow intermingled with *T. ulmifolia,* a widespread polymorphic complex containing forms that resemble *T. hermannioides.* A crossing program between *T. hermannioides* and diploid and tetraploid varieties of *T. ulmifolia* revealed barriers to hybridization particularly in crosses at the diploid level. It is concluded that *T. hermannioides* is a restricted diploid species that is reproductively isolated from *T. ulmifolia.*

Distyly is reliably reported from 23 flowering plant families (Ganders, 1979). In taxa on which experimental work has been undertaken, it has usually been shown that the stamen-style dimorphism is closely associated with a diallelic self-incompatibility system as well as several morphological polymorphisms involving pollen size, pollen production, and stigmatic papillae number and length. Although there is general agreement that distyly is an outbreeding mechanism (Darwin, 1877; Crowe, 1964; Vuilleumier, 1967), the functions of the various floral polymorphisms that accompany self-incompatibility are still unclear (Yeo, 1975; Ganders, 1979).

The large neotropical genus *Turnera* (Turneraceae) contains some 54 species of which 37 are reported to be heterostylous (Urban, 1883). Species within the genus are poorly defined, and there is need for a modern taxonomic revision of the group. With the exception of studies of distyly in the widespread polymorphic weed complex *T. ulmifolia* L. (including the synonyms *T. subulata* Smith and *T. trioniflora* Sims) by Lock (1904), Barrett (1978), and Bentley (1979), there are no published reports of experimental work on the reproductive biology of species of *Turnera.* To broaden understanding of the nature of distyly in the genus, we initiated a study of the breeding system of *T. hermannioides,* a herbaceous to woody perennial native to northeastern Brazil. In addition to documenting general features of distyly, incompatibility relationships, and population structure in the species, we also investigated its crossing relationships with *T. ulmifolia,* with which it is superficially similar in habit (Urban, 1883) and frequently sympatric.

MATERIALS AND METHODS

All populations of *Turnera hermannioides* studied occur in the state of Sergipé in northeastern Brazil. Detailed localities are presented in Table 1. At each population, the number of long- and short-styled plants was recorded. In populations 2, 3, and 4, the entire flowering population was scored whereas in population 1, a complete sample of the accessible part of the population (ca. one-third of the total size) was made (Table 5). Deviations from the expected 1 : 1 morph frequency were analyzed using the G-statistic which was calculated for each population. In addition, pooled and heterogeneity G-statistics were calculated (Sokal & Rohlf, 1981) to examine whether population structures were similar.

[1] We thank the staff of the herbarium at the Instituto Pesquisas Agronomicas, Recife, Pernambuco for assistance, NSERC Canada for funding field studies in northeastern Brazil, and Maria Mercedes Arbo for aid in securing seed collections of *Turnera ulmifolia.* This paper is dedicated to the memory of the late Professor Dárdano de Andrade-Lima, authority on the flora and vegetation of northeastern Brazil, who introduced one of us to *Turnera.*

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TABLE 1. Localities of *Turnera hermannioides* and *Turnera ulmifolia* populations used in this study. All populations of *T. hermannioides* were collected along roadsides on open, waste ground.

A. *Turnera hermannioides*

Population	Locality	Varieties of *T. ulmifolia* Present at Site
1[a]	Hwy. 235, ca. 30 km W of Itabaiana, Sergipé	*elegans*
2	Hwy. 235, ca. 15 km W of Itabaiana, Sergipé	*elegans*
3	Hwy. 235, ca. 1 km W of Itabaiana, Sergipé	*elegans*
4[b]	Hwy. 235, 21 km S of BR101, near Aracaju, Sergipé	*elegans* and *surinamensis*

B. *Turnera ulmifolia*

Variety	Locality	Chromosome Number and Ploidy Level[c]
surinamensis	Santarém, Pará, Brazil	$2n = 2x = 10$
grandiflora	Corrientes, Argentina	$2n = 2x = 10$
intermedia	Barreirinhas, Maranhão, Brazil	$2n = 2x = 10$
intermedia	St. Cristobal, Dominican Republic	$2n = 4x = 20$
elegans	Crato, Ceara, Brazil	$2n = 4x = 20$

[a] Vouchers for chromosome counts, Shore and Barrett 1 TRT.
[b] Vouchers for chromosome counts, Shore and Barrett 2 TRT.
[c] Vouchers for chromosome counts, Shore and Barrett (unpubl. data).

At population 1, ten flowers of each style form were collected and the style length, stamen length, and corolla diameter were measured with calipers to the nearest 0.1 mm (Table 2). Style and stamen lengths were measured from the base of the ovary to the top of the male or female reproductive organ. Flower buds, 2–4 mm in length, were collected and fixed in 3:1 ethanol:acetic acid for chromosome number determination. Later, anther squashes were prepared in 2% aceto-carmine, and meiosis was observed in pollen mother cells. Eighteen larger buds were collected separately from 18 individuals of each style morph to determine pollen production. Pollen counts were made using the hemacytometer method of Lloyd (1965). Anthers from three buds per morph were pooled for each value obtained. Six replicate samples were then determined for each morph. Data were analyzed by nested ANOVA.

A bulk seed sample was collected at population 4 where ample ripe seed was available. The seed was sown in the summer of 1982 in a soil mixture of 3 parts sterilized potting compost (1 peat:1 clay-loam:1 sand):1 sand:1 peat, in 7.5 cm plastic pots. Seeds were covered with about 1 cm soil and allowed to imbibe water for one week. As the soil was allowed to dry, germination proceeded. Nine short-styled and 13 long-styled plants were obtained. When they had reached the 5-leaved stage, these were then transplanted into 12 cm clay pots and grown under uniform glasshouse conditions in air temperatures ranging from 25°–35°C. The plants were the material used for experimental work described below.

The polar and equatorial axes of five pollen grains were measured for each of seven individuals per morph. Pollen grains were measured to the nearest 1.5 μm using a calibrated ocular micrometer on a compound microscope. Nested ANOVA was used to examine variation among individuals and between style morphs.

A controlled crossing program was initiated in May 1983, to determine the compatibility relationships of the floral morphs (Table 4). Each individual was self-pollinated at least twice, crossed to at least two different individuals of the same floral morph, and to a minimum of two individuals of the opposite floral morph. Pollinations were performed in a pollinator-free glasshouse. Pollen was transferred from the male to the female parent by removing all stamens with a pair of clean, fine forceps and rubbing the dehiscent anther sacs on recipient stigmas. The number of seeds set per pollination was recorded. For inter-morph crosses, capsules were harvested prior to dehiscence, which normally occurred approximately 24 days after pollination, and dis-

TABLE 2. Floral characters in the long- and short-styled morphs of *Turnera hermannioides*. Values are the mean and standard deviation. Measurements of floral organs and pollen production were made from field grown plants in population 1, the remaining characters were from glasshouse grown plants originating from seed collected in population 4. NS = not significant.

Character	Floral Morph		*F*	*P*
	Long-styled	Short-styled		
Flower diameter (mm)	33.9 ± 2.8	34 ± 5.1	0.007	NS
Style length (mm)	12 ± 1.1	7.3 ± 0.9	114.0	<0.001
Stamen length (mm)	7.3 ± 0.6	12 ± 0.8	221.0	<0.001
Pollen size (μm) (polar axis)	63.6 ± 2	72.9 ± 2.6	61.7	<0.001
Pollen size (μm) (equatorial axis)	33 ± 0.9	39.6 ± 1.5	117.0	<0.001
Pollen production$^{-flower}$	15,200 ± 2,700	11,800 ± 2,200	6.14	<0.05
Ovule number$^{-flower}$	32.3 ± 9.9	39 ± 8.8	2.4	NS
Seeds$^{-capsule}$ [a]	20 ± 10.1	18.9 ± 10.1	0.14	NS

[a] Following inter-morph pollination.

sected open. This procedure enables determination of the number of seeds set and the total number of ovules produced in a flower. Data on seed set and ovule number were analyzed by nested ANOVA using a sample of nine individuals of each morph and two replicate measures for each individual.

A second crossing program was initiated in June 1983, to determine the crossing relationships of *T. hermannioides* with taxa in the related *T. ulmifolia* complex (Table 6). Five population samples of four varieties were used. Five individuals from each population, including *T. hermannioides* were used. The varietal status, locality, and ploidal level of members of the *T. ulmifolia* complex are provided in Table 1. Further details of the reproductive biology of populations are presented in Barrett (1978). Pollinations were performed as described above. Capsules were harvested after dehiscence. Seeds were retained in the capsules by placing parafilm over the swollen ovary about ten days after pollination. For each cross the number of brown plump seeds produced per pollination was recorded.

RESULTS

Floral morphology. Flowers of *Turnera hermannioides* exhibit a precise reciprocality in the lengths of stamens and styles between the long- and short-styled morphs (Table 2). There was no significant difference between the floral morphs in flower diameter, number of ovules per flower, and seed set following legitimate (intermorph) pollination. In common with many distylous plants, *T. hermannioides* exhibited dimorphism in the size of pollen grains. Both axes of pollen grains are longer in the short-styled morph. Pollen production per flower in the long-styled morph was significantly higher than in the short-styled morph (Table 2). Microscopic observation of stigmas of the floral morphs revealed the absence of stigmatic papillae, a feature shared with *T. ulmifolia*, and in contrast to most heterostylous species.

Where appropriate data were available, nested ANOVAs were undertaken on reproductive traits in order to partition the observed variation into the three possible sources (among morphs, among individuals, and error). In our samples, significant variation occurred in ovule number per flower among individuals, but not between the floral morphs (Table 3). Large samples clearly would be required to determine if morph-specific differences in ovule number occur. The data for ovule number and pollen production suggest that

TABLE 3. Variance components of reproductive characters in *Turnera hermannioides*. Values are the percentage of the observed variation which is attributable to individual variation, floral morph, and error following nested analysis of variance.

Character	Individual	Morph	Residual
Ovule number	70[b]	13	17
Pollen production	40[b]	38[a]	22
Pollen size (polar axis)	9[b]	85[b]	6

[a] $P < 0.05$.
[b] $P < 0.001$.

TABLE 4. Fruit and seed set following controlled self, intra-morph and inter-morph cross-pollination of the long- and short-styled morphs of *Turnera hermannioides*. Plants were grown from seed collected in population 4; all pollinations were performed under glasshouse conditions.

Pollination Treatment	No. of ♀ Plants	No. of Flowers Pollinated	% Fruit Set	No. of Seeds Produced	Mean Seed Set per Capsule ± s.d.
L self	13	87	10	13	1.4 ± 0.7
S self	9	62	13	10	1.3 ± 0.7
L × L	13	28	25	7	2.3 ± 0.3
S × S	9	18	6	1	1
L × S	13	27	100	540	20 ± 10.1
S × L	9	18	100	341	18.9 ± 10.1

considerable individual variation in fertility may exist within populations of *T. hermannioides*.

Compatibility relationships. The controlled pollination program demonstrated the presence of a physiological self-incompatibility system in *T. hermannioides*. Self- and intra-morph pollinations resulted in relatively small amounts of seed being produced. In contrast, legitimate pollinations were highly fertile and all pollinations resulted in capsules and seed (Table 4).

Population structure. Morph frequencies within populations of *T. hermannioides* are isoplethic (equal proportions) and the pooled and heterogeneity G-statistics indicate the absence of heterogeneity among populations (Table 5). Presumably, this equilibrium is maintained by disassortative mating between the floral morphs as a result of the strong diallelic incompatibility system.

Crossability with Turnera ulmifolia. Observations of meiosis in plants of *T. hermannioides* from populations 1 and 4 indicated that they were both diploid ($2n = 2x = 10$) with regular bivalent formation. Results of the crossing program to investigate the biosystematic relationships between *T. hermannioides* and members of the *T. ulmifolia* complex are presented in Table 6. Crosses between the two taxa usually resulted in the initiation of capsules, however, fruits and developing seed commonly aborted after initial swelling. Barriers to crossability were particularly evident between diploid varieties of *T. ulmifolia* and *T. hermannioides*. Although approximately one-third of the pollinations that were conducted resulted in fruit, little seed was formed. Interestingly, significant numbers of seed were produced when *T. hermannioides* was used as the male parent in crosses with the two tet-

TABLE 5. Representation of floral morphs in four populations of *Turnera hermannioides* in Sergipé, northeastern Brazil. NS = not significant.

Population	No. of Long-styled Plants	No. of Short-styled Plants	G[a]	df	P
1	60	57	0.08	1	NS
2	54	56	0.04	1	NS
3	60	53	0.43	1	NS
4	47	61	1.82	1	NS
Total	221	227	2.37	4	NS

[a] G (pooled) 0.08, df 1, NS; G (heterogeneity) 2.29, df 3, NS.

TABLE 6. Seed fertility in reciprocal crosses between *Turnera hermannioides* (population 4) and varieties of *Turnera ulmifolia*. All pollinations were performed under glasshouse conditions.

Varieties and Ploidy Level	No. of Pollinations	% Fruit Set	Mean Seed Set per Pollination ± s.d.
A. *T. hermannioides* as ♀ parent			
surinamensis (2*x*)	9	56	1.8 ± 2.6
grandiflora (2*x*)	12	25	0.4 ± 0.8
intermedia (2*x*)	8	25	0.8 ± 1.8
intermedia (4*x*)	6	83	4.3 ± 2.7
elegans (4*x*)	6	33	1.3 ± 1.8
B. *T. hermannioides* as ♂ parent			
surinamensis (2*x*)	10	30	1 ± 1.7
grandiflora (2*x*)	11	36	1.3 ± 2.1
intermedia (2*x*)	9	22	0.3 ± 0.7
intermedia (4*x*)	7	100	8.3 ± 3.6
elegans (4*x*)	7	71	13 ± 10.1

raploid varieties of *T. ulmifolia*. The reciprocal crosses were less productive. The crossing program demonstrates that *T. hermannioides* is, in large part, reproductively isolated from *T. ulmifolia* at the diploid level. Although F_1 plants may be produced from crosses with tetraploid varieties, they would be triploid and probably sterile.

Discussion

Apart from the absence of stigmatic polymorphisms, the distylous syndrome of *T. hermannioides* resembles those described in several other heterostylous families (reviewed in Ganders, 1979). The corolla morphology of distylous *Turnera* species is unusual for heteromorphic taxa because of the absence of a well-developed corolla tube. Flowers of *T. hermannioides* and *T. ulmifolia* are bowl-shaped and relatively unspecialized. Observations of visitors to flowers of both species indicated that they were visited by a wide range of insects, including *Apis mellifera, Xylocopa* sp., and various groups of solitary bees (see Barrett, 1978). It seems likely that with relatively generalized insect visitors and unspecialized flowers, considerable illegitimate pollination would occur, particularly in plants with large floral displays. The strongly developed self-incompatibility system in *T. hermannioides* and *T. ulmifolia* (Barrett, 1978) may thus be maintained to prevent self-fertilization.

There is little information on the geographic distribution of *T. hermannioides*. Based on our own field observations, as well as surveys of herbarium collections from Brazil, it would appear that the species occurs in scattered localities in the states of Sergipé, Bahia, and Minas Gerais. Diploid varieties of *T. ulmifolia* in Brazil also exhibit restricted and widely scattered distributions, frequently in association with local soil conditions. In striking contrast, polyploid varieties of the *T. ulmifolia* complex are ruderal weeds with broad ecological tolerance and widespread distributions (Barrett, 1978; Bentley, 1979). Throughout northeastern Brazil, the tetraploid *T. ulmifolia* var. *elegans* is conspicuous as a weed of waste ground and roadsides, including those in which *T. hermannioides* occurs. Although *T. ulmifolia* var. *elegans* occurred intermingled with *T. hermannioides* in the four populations sampled, no putative hybrids were observed. While small numbers of seed may be produced from crosses between the two taxa all attempts by us to obtain viable seedlings have failed. The taxa are reproductively isolated from one another.

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THE PLANTS OF 'OCOQUILI' ISLAND, SAN BLAS COAST, PANAMA[1]

W. G. D'Arcy and Barry Hammel[2]

Abstract

Study of one of the few San Blas Islands (Panama) with intact vegetation indicates that the flora has a greater affinity with distant circum-Caribbean islands than with the nearby mainland.

The San Blas coast of northeastern Panama is fringed by a series of small flat islands, few of them as long as 1 km, and few more than 1 km offshore. Nothing is known about the vegetation of the islands before they were settled by the Kuna Indians in the middle of the last century (Jaén, 1978). Today most of the islands are densely populated without a single trace of original plant life remaining. On 9 October 1978, we hired an outboard motor boat and visited a small island in the group that was uninhabited and appeared to have a large measure of its natural vegetation intact. The 34 species noted during this morning included two new to Panama and an assemblage of species more likely to be found on a flat limestone island in the northern Caribbean hundreds of miles away than on the mainland of Panama less than 1 km away.

The island's location, 9°14′N, 48°01′45″W, is midway between Isla Nustupo and Ailigandí, and it is approximately halfway along the San Blas coast between Porvenir, the district capital, and Puerto Obaldía at the Colombian frontier. It is only a few hundred meters from the mainland. This island is not marked on any maps we consulted, and we refer to it by the name given by our Indian guides, 'Ocoquili,' which refers to the coconut trees on it. Upon leaving the area later in the day, we persuaded our pilot to circle 'Ocoquili' and the photo shown here (Fig. 1) was taken.

Ocoquili Island is about 1 km long and 300–400 m wide, and it is formed of coquina-like limestone. Coconuts grow around most of the edges, and on the western end there is an accumulation of sand. Much of the interior is low and flooded, covered by mangroves. Across the island toward the eastern end is a shallow channel and holes in the partly emergent limestone, at the edges of this, harbored small plants.

Although no one lived there at the time, our guides reported that boatmen sometimes visited the island for coconuts, fishing, parties, and other reasons but did not stay long at a time. We found no signs of construction and no sign of feral animals.

A total of 37 collections were made, some of them sterile. Determinations of Gramineae and Cyperaceae were made by Gerrit Davidse, of Rubiaceae by John D. Dwyer, and the balance by the senior author. Thirty-three species were represented, and the sight record of *Cocos nucifera* yielded a total of 34 species (Table 1). Although more species may be present, none were apparent at the time of this visit even in sterile condition. Our coverage was nearly complete. All collections are deposited with the Missouri Botanical Garden (MO).

Of the trees, three species are mangroves. Red, white, and black mangroves were all present, but we found only one species of red mangrove, *Rhizophora mangle.* Of the other tree species, *Hippomane mancinella* is neotropical, *Cocos nucifera* is introduced, and *Cordia sebestena,* commonest in the northern Caribbean, has been collected few times in Panama, and then only along this same San Blas coast. All tree species are mainly known from neotropical seacoasts, although some range inland in gallery forests, and all are to be found in proximity in many Caribbean sites (Table 2).

The shrubs have pan-Caribbean distribution, although some also occur elsewhere. *Conocarpus erecta* and *Dalbergia ecastophyllum* are found near many Caribbean coastlines, and they also occur in West Africa. *Suriana maritima,* which

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TABLE 1. List of the 34 species found on 'Ocoquili' Island, San Blas Coast, Panama. Sources: Rubiaceae from Dwyer (1980), Boraginaceae from Miller (in prep.), Amaranthaceae from Mears (1982), and other distributions from Adams (1972).

Species	Family	Habit	Range	Habitat-Ecology
Andropogon bicornis L.	Gramineae	herb	neotropical	weed species
Avicennia germinans (L.) L.	Verbenaceae	tree	neotropical, W Africa	limestone coasts
Blutaparon vermiculare (L.) Mears	Amaranthaceae	herb	neotropical	coastlines
Canavalia maritima (Aubl.) Thou.	Leguminosae	herb	pantropical	coastal strands
Cassine xylocarpa Vent.[a]	Celastraceae	shrub	N Caribbean	dry woodlands
Chamaesyce mesembrianthemifolia Jacq.[b]	Euphorbiaceae	herb	neotropical	calcareous coasts
Chiococca alba (L.) Hitchc.	Rubiaceae	vine	Texas to Argentina	limestone
Cissus sicyoides L.	Vitaceae	vine	neotropical	weed species
Coccoloba uvifera L.	Polygonaceae	tree	Caribbean	seacoasts
Cocos nucifera L.	Palmae	tree	introduced	seacoasts
Conocarpus erecta L.	Combretaceae	shrub	neotropical, W Africa	coastal
Cordia sebestena L.[b]	Boraginaceae	tree	N & W Caribbean	seacoasts
Crinum erubescens Ait.[c]	Amaryllidaceae	herb	introduced	shorelines
Cuervea kappleriana (Miq.) A.C. Sm.	Hippocrateaceae	vine	neotropical	coastal woodlands
Dalbergia brownei (Jacq.) Urb.	Leguminosae	shrub	Caribbean to Brazil	coastal woodlands
Dalbergia ecastophyllum (L.) Taub.	Leguminosae	shrub	neotropical, W Africa	seacoast thickets
Eustachys petrea (Sw.) Desv.[b]	Gramineae	herb	neotropical	limestone & beaches
Fimbristylis cymosa R. Br.	Cyperaceae	herb	pantropical	coastal areas
Hippomane mancinella L.	Euphorbiaceae	tree	neotropical	coastlines
Laguncularia racemosa (L.) Gaertn. f.	Combretaceae	tree	neotropical, W Africa	mangrove
Lantana involucrata L.[b]	Verbenaceae	shrub	Caribbean	limestone & coasts
Melanthera aspera (Jacq.) Benth.	Compositae	herb	Caribbean, Ecuador	seacoasts
Pavonia rhizophorae L.[b,c]	Malvaceae	herb	Panama to Colombia	seacoasts
Pilea microphylla (L.) Liebm.	Urticaceae	herb	pantropical	weed species
Randia aculeata L.	Rubiaceae	shrub	Mexico to Venezuela	dry limestone
Rhizophora mangle L.	Rhizophoraceae	tree	neotropical, W Africa	mangrove
Sesuvium portulacastrum L.	Aizoaceae	herb	pantropical	seashores
Sophora tomentosa L.[b]	Leguminosae	shrub	pantropical	coastal weed
Spartina spartinae (Tru.) Merr.[c]	Gramineae	herb	Texas to Argentina	coasts & marshes
Sporobolus virginicus L.	Gramineae	herb	pantropical	shores
Stenotaphrum secundatum (Walt.) Gaertn. f.[b]	Gramineae	herb	pantropical	limestone coasts
Suriana maritima L.[a]	Simaroubaceae	shrub	Caribbean, Indian & Pacific Oceans	seacoasts
Vigna luteola (Jacq.) Benth.	Leguminosae	herb	pantropical	limestone coasts
Wedelia trilobata (L.) Hitchc.	Compositae	herb	neotropical, W Africa	weed species

[a] New report for Panama.
[b] In Panama, found only nearby on this coast.
[c] Not on Jamaica.

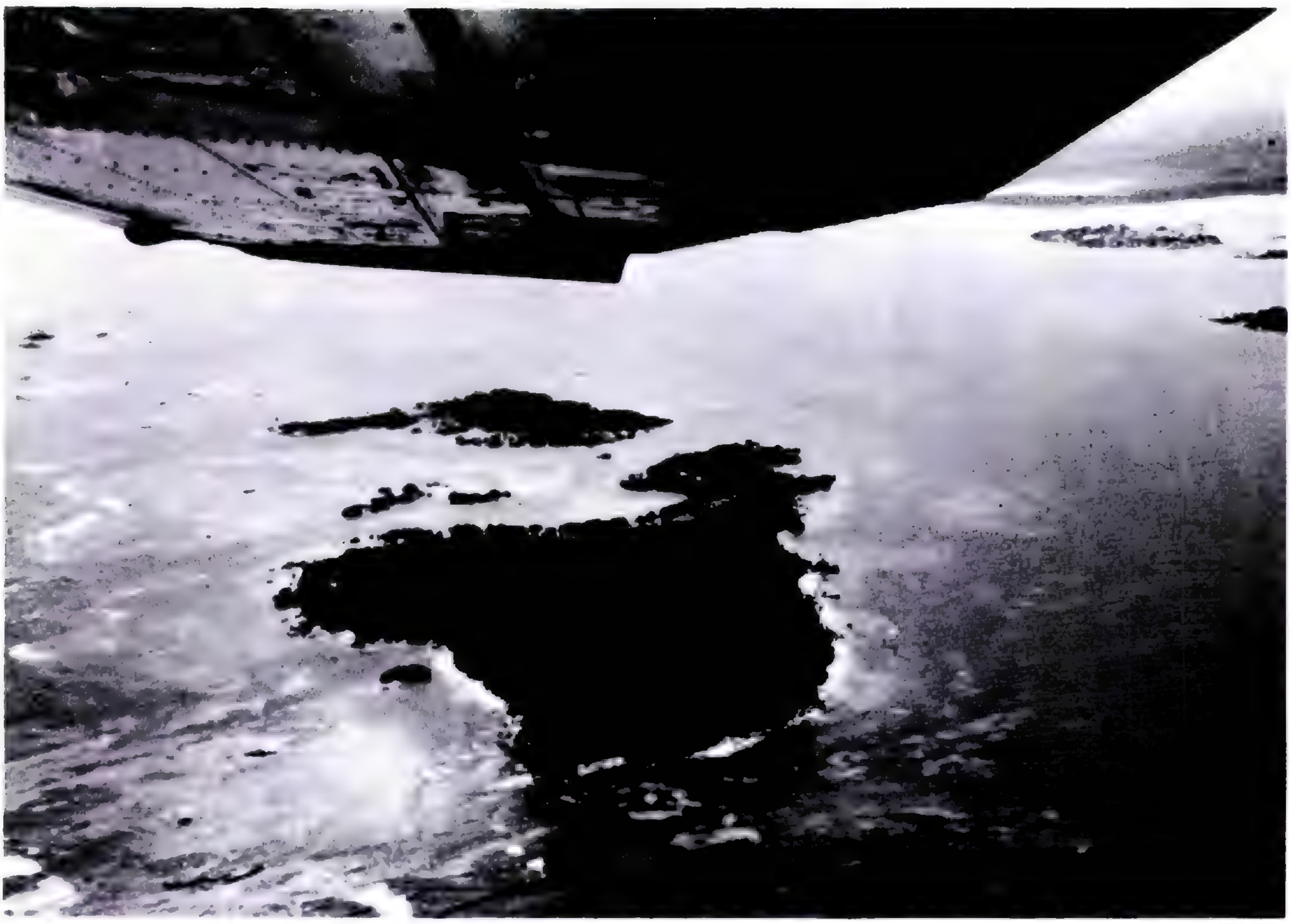

FIGURE 1. Aerial view of 'Ocoquili' Island.

is a new record for Panama, is found on seacoasts in the area and also in the Indian Ocean and South Pacific. *Dalbergia brownei* ranges around the Caribbean coast to Brazil where it occurs inland along gallery forests. *Lantana involucrata* is particularly common near shorelines of flat calcareous islands of the eastern Caribbean, but it also occurs inland in some places. *Randia aculeata* is used as a Christmas tree in some Caribbean islands: it occurs inland in Panama as well as along the coasts.

There are only three species of climbing vines; two of them, *Chiococca alba* and *Cissus sicyoides,* are pantropical and also plentiful in the Antilles, and *Cuerva kappleriana* is restricted to the Caribbean area. Several of the herb or shrub species might also be called vines: *Dalbergia brownei,* which has tendrils, *Vigna luteola,* and *Canavalia maritima,* but these do not usually ascend over other vegetation, and they do not do so on Ocoquili. No epiphytes were found.

TABLE 2. Growth forms on 'Ocoquili' Island.

Trees	7
Shrubs	8
Herbs	16
Climbing vines	3
Total species	34

Only two species, *Cocos nucifera* and *Crinum erubescens,* are introduced. Two of the species, *Cassine xylocarpa* and *Suriana maritima,* are new reports for Panama, and eight species are known in Panama only from sites along this coast. All but three species, *Crinum erubescens, Pavonia rhizophorae,* and *Spartina spartinae,* are known from Jamaica, more than 900 km to the north, and the last of these is widespread on calcareous coasts in the Caribbean area and on alkaline flats in inland continental areas.

While the florula of the tiny Ocoquili Island is but a token representation of the flora that once covered this string of numerous islands, it is sufficient to indicate that there was an important circum-Caribbean coastal element that formed an assemblage of species distinct from the associations now known on the mainland.

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ANTIRHEA AROMATICA (RUBIACEAE, GUETTARDEAE), A NEW SPECIES FROM VERACRUZ, MEXICO[1]

GONZALO CASTILLO-CAMPOS[2] AND DAVID H. LORENCE[3]

ABSTRACT

A new species of Rubiaceae, *Antirhea aromatica* Castillo-Campos & Lorence, is described from central Veracruz, Mexico. A tree of the tropical semideciduous forest, it appears to be very localized in distribution and is the first record of the genus for Veracruz. Its distribution, habitat, and affinities are discussed, and specimen citations are given.

RESUMEN

Se describe una nueva especie de Rubiaceae, *Antirhea aromatica* Castillo-Campos & Lorence, del centro de Veracruz, México. Se trata de un árbol que crece en la selva mediana subperennifolia, con área de distribución muy restringida y además se registra el género por primera vez para Veracruz. Se discute su distribución, hábitat y afinidades, y se citan los ejemplares examinados.

During the course of studies on Mexican Rubiaceae and on the vegetation around Jalcomulco in central Veracruz, several collections were encountered which represent an undescribed species of *Antirhea* of the tribe Guettardeae. Members of the Guettardeae are characterized by having a two- to many-locular ovary in which each locule has a single anatropous ovule, a corolla with the stamens inserted in the throat, and a usually cymose inflorescence. *Antirhea* Comm. ex A. L. Juss. is distinguishable from the other neotropical genera in the tribe by the following combination of characters: an axillary, usually dichotomous, cymose inflorescence, a corolla with strongly imbricate lobes, one or two of them being exterior, included anthers, and a drupaceous fruit with two to nine cells and a deciduous calyx (Standley, 1934).

Our species is readily accommodated into both the Guettardeae and *Antirhea* itself. Its biflorous inflorescence represents a dichotomous cyme where each inflorescence branch has been reduced to a single flower. Such biflorous cymes, as well as those reduced to solitary flowers, also occur in a number of Antillean *Antirhea* species (Standley, 1934).

Antirhea is a genus of about 50 species distributed in the Paleotropics of Madagascar, the SW Indian Ocean islands (Comores, Mascarenes), W India, Asia, Indonesia and Australia, and also in the American tropics where it is best represented in the Antilles. Standley (1934) recognized 31 American species, most of which occur in the larger islands of Cuba, Hispaniola, Jamaica, and Puerto Rico. One Antillean species, *A. lucida* (Sw.) Benth. & Hook., reaches Mesoamerica where it has been reported from Belize (Standley & Williams, 1975), Guatemala, and more recently from Quintana Roo in Mexico (Téllez V. & Sousa S., 1982). A second species, *A. trichantha* (Griseb.) Hemsl., is known only from Panama (Dwyer, 1980). Our new species represents the first report of the genus from Veracruz.

The majority of *Antirhea* species appear to have extremely restricted distribution patterns, i.e., most are endemic to a single island or are known only from the type locality. As Veracruz and the adjacent states have been relatively well collected, the new species may be endemic to the state.

Antirhea aromatica Castillo-Campos & Lorence, sp. nov. TYPE: Mexico. Veracruz: Municipality of Jalcomulco; ca. 10 km S of Apazapan, Barranca de Monterrey, S of Cuetzalan, between Cuetzalan and Apazapan;

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semideciduous forest, 350 m, 17 Sept. 1983 (fl, fr), *Castillo-Campos 2957* (holotype, XAL; isotypes, MEXU, XAL). Figure 1.

Arbor 6–15 metralis lenticellata. Folia petiolata; lamina elliptica vel ovato-elliptica glabrata 90–200 mm longa 40–90 mm lata. Inflorescentiae axillares biflores; pedunculus 20–45 mm longus. Flores sessiles pubescentes; cupula calycis 5–6 mm longa, lobis calycis 4–5 triangularibus subulatis 4–8 mm longis; corolla alba aromatica, tubo 90–117 mm longo, lobis 4–5, 10–16 mm longis; antherae 4–5 ca. 8 mm longae. Fructus baccatus pubescens resinosus elliptico-oblongus 25–37 mm longus 10–17 mm latus, costulis longitudinalibus 6–8 prominentibus; semina 7–10 cylindrica 25–30 mm longa.

Trees 6–15 m tall, 10–30 cm dbh, the bark whitish, flaking near the base, the blaze pinkish with white rays, the wood yellow. Stems brownish, lenticellate, 3–4 mm diam., the internodes crowded apically, the new growth hirtellous, resinous; stipules caducous, brown, resinous, ovate-deltoid, naviculate, 11–14 mm by 5–7 mm, the apex acute to acuminate, the broad margins scarious, externally hirtellous, internally pilose basally, lined with a deltoid patch of digitate glands, each 0.5–0.6 mm long. Leaves in subequal pairs, petiolate; petioles 15–60 mm by 0.8–1 mm, hirtellous, slightly canaliculate adaxially; lamina elliptic to ovate-elliptic, 90–200 mm by 35–90 mm, the apex shortly acuminate or rarely acute, the acumen 5–20 mm long, usually falcate, the base narrowly cuneate to cuneate, often more or less attenuate, the sides subequal, the secondary veins 6–8 pairs, festooned brochidodromous, the ultimate venation prominently reticulate, visible on both surfaces, chartaceous, slightly discolorous, drying brownish or greenish, both surfaces appressed hirtellous-hirsutulous especially when young, glabrescent, the costa and veins hirsutulous, the secondary vein axils barbate abaxially, the margin ciliolate, callose. Inflorescence axillary, several generally produced near the branch apex, each with 2 flowers; peduncle 20–45 mm by 0.8–1.2 mm, appressed hirtellous. Flowers sessile, each subtended by 1(–2) persistent often bilobed ovate-naviculate involucral bracts 5–8 mm by 4–6 mm, acute, carinate, the margins scarious, each lined with a deltoid patch of digitate glands; hypanthium obconical, 2–2.5 mm long, tomentose; calyx cup 5–6 mm long, tubular, externally sparsely hirsutulous, internally with 5 deltoid patches of digitate glands alternating with the lobes; calyx lobes (4–)5, deltoid-subulate, 4–8 mm by 1.5–2.5 mm basally, externally sparsely hirsutulous. Corolla white, aromatic when fresh, salverform, the tube cylindrical, 90–117 mm long by 4–5 mm wide medially, externally hirsutulous, more or less resinous basally, the lobes (4–)5, imbricate in bud, ovate-elliptic, 10–16 mm by 5–7 mm, obtuse, externally hirsutulous, internally glabrous, recurved at anthesis, the margin undulate; stamens (4–)5, interlobular, sessile, affixed ca. 5 mm below the faux; anthers linear-subulate, 8–9 mm by 1 mm, the base cordate, the apex acute, exserted for 2–3 mm; style 40–70 mm long, sparsely spreading-hirsutulous; ovarian disc 1.5 mm long, doughnut shaped; ovary 7–10-locular, the ovules pendulous. Fruit drupaceous, obovoid-ellipsoid, 25–37 mm by 10–17 mm, 6–8-costate, sparsely hirtellous, resinous, the pericarp thin, fleshy, yellowish when ripe, the calyx ultimately deciduous; seeds 7–10, tightly adherent, narrowly ellipsoid, 25–30 mm by 3–5 mm medially, more or less curved, the testa tough, spongy; embryo cylindrical.

Distribution. The species is known only from the type locality in central Veracruz, near the towns of Jalcomulco and Apazapan in the municipality of Jalcomulco at altitudes of 350–500 m.

Specimens examined. MEXICO. VERACRUZ: Municipality of Jalcomulco, ca. 10 km S of Apazapan, Barranca de Monterrey, S of Cuetzalan, between Cuetzalan and Apazapan, 350 m, *Castillo C. 2987* (XAL), *Robles 248* (XAL); vicinity of Jalcomulco, ca. 500 m, 25 July 1973, *Gándara & Dorantes 90* (F, MEXU, MO).

In addition, ca. 50 more isotypes will be distributed shortly to a wide range of herbaria.

Phenology. Flowering occurs during July and August; the fruits are produced concurrently and ripen in October. The somewhat fleshy, yellow pericarp suggests bird dispersal, although no recent regeneration was observed locally.

The specific epithet refers to the strong, gardenia-like fragrance produced by the flowers in the evening. This, together with the long, tubular white corollas, is characteristic of plants with a hawkmoth pollination syndrome. The patches of digitate glands within the stipules, floral bracts, and calyx tube apparently produce the brown resin that bathes the young developing organs and is presumably protective in nature. The resin is highly aromatic when dissolved in alcohol, to which fact the epithet also alludes. This resin also occurs in a number of Antillean species.

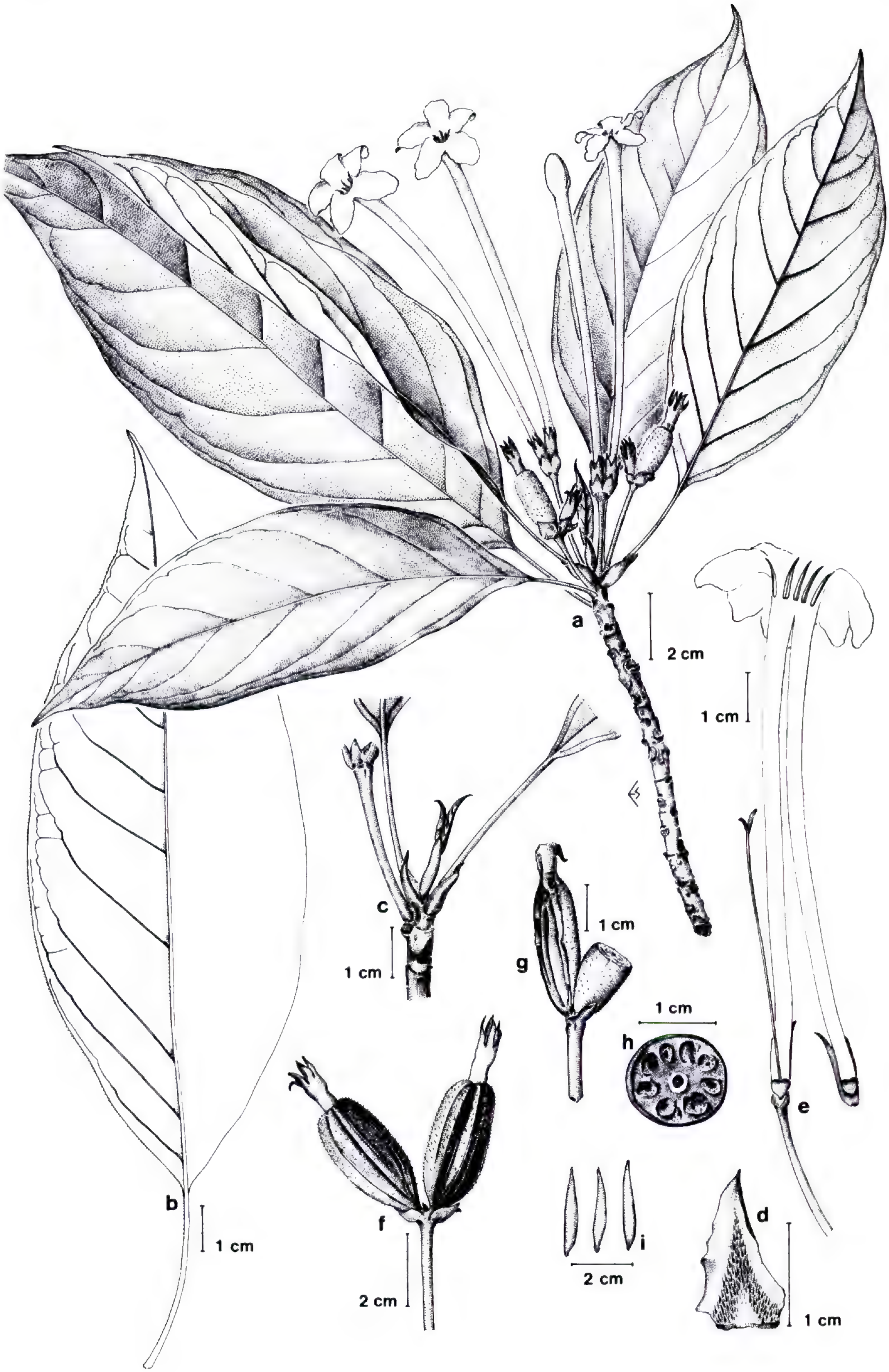
a
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TABLE 1. Some diagnostic morphological characters of the two species of *Antirhea* known from Mexico.

Character	*A. aromatica*	*A. lucida*
Vegetative pubescence	hirtellous-hirsutulous	glabrous
Resin	present	absent
Stipule size (mm)	11–14 by 5–7	4–7 by 1.5–2
Petiole length (mm)	15–60	3–10
Lamina size (mm)	90–200 by 35–90	45–65 by 20–35
Number of secondary vein pairs	6–8	10–11
Number of flowers per inflorescence	2	22–30
Calyx length, total (mm)	10–14	2–3
Corolla tube length (mm)	90–117	4–5
Fruit size (mm)	25–37 by 10–16	5–7 by 3–4

Common name. "Chicahuastle."

Uses. The wood is said to be used locally for construction of houses.

Habitat. The area around Jalcomulco and Apazapan is characterized by series of limestone hills and canyons with altitudes ranging from 350 to 1,000 m dissected by a river system. The limestone outcrops are covered with a thin, black clay soil displaying rapid runoff during rains. The area was originally covered by low, seasonally deciduous tropical forest intergrading with areas of taller semideciduous tropical forest in canyons and on slopes. Much of this forest has been converted for sugar cane and mango plantations. Characteristic arboreal components of the low deciduous forest are: *Bauhinia divaricata* L., *Bursera simaruba* (L.) Sarg., *Calliandra* spp., *Comocladia engleriana* Loes., *Diospyros veraecrucis* Standley, *Diphysa robinioides* Benth., *Pistacia mexicana* H.B.K., *Plumeria rubra* L., and *Spondias* sp., *Opuntia* spp., and columnar cacti, as well as *Hechtia* spp., abound in the lower stratum and understory. Dominant tree species of the taller semideciduous forest include: *Brosimum alicastrum* Sw., *Bursera simaruba* (L.) Sarg., *Hyperbaena mexicana* Miers, *Manilkara zapota* (L.) Van Royen, and *Protium copal* (Schldl. & Cham.) Engl.

Diversity of woody species is high in the area, which may be partly due to the series of ecotones between the two forest types. *Antirhea aromatica* occurs only in the most humid canyons where it is a fairly common mid-stratum component of the tropical semideciduous forest.

Antirhea aromatica is easily distinguished from *A. lucida*, the only other species to occur in Mexico and northern Mesoamerica, by the characters listed in Table 1. It differs from the other Antillean members of the genus by its larger, thinner leaves and much larger flowers and fruits. Its closest relative appears to be *A. involucrata* Urban & Ekman from Hispaniola, which also grows on limestone, is resinous, and has a two-flowered involucrate inflorescence with a relatively large corolla and fruit. The latter species differs by its thicker glabrous leaves, a smaller subsessile inflorescence, and smaller flowers and fruits with a 5–6-celled ovary. The Panamanian *A. trichantha* differs in having a densely puberulent, many-flowered panicle and much smaller flowers and fruits.

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FIGURE 1. Habit and details of *Antirhea aromatica* Castillo-Campos & Lorence.—a. Habit, with flowers and fruits.—b. Detail of leaf, showing venation.—c. Detail of branch apex, showing stipules, petioles, and floral peduncle.—d. Stipule, internal surface showing patch of resin glands.—e. Detail of opened flower.—f. Detail of mature fruits.—g. Mature fruits, sectioned longitudinally and transversally.—h. Transverse section of mature fruit.—i. Seeds. Illustration by E. Saavedra (INIREB), based on *Castillo-Campos 2957*.

THREE NEW SPECIES OF *RHIPIDOCLADUM* FROM MESOAMERICA[1]

RICHARD W. POHL[2]

ABSTRACT

Rhipidocladum clarkiae Pohl and *R. pacuarense* Pohl are described from Costa Rican flowering material and *R. panamense* Pohl is described from flowering specimens from Panama.

The genus *Rhipidocladum* was erected by McClure (1973) to include species of bamboos previously assigned to *Arthrostylidium, Arundinaria,* and *Ludolphia.* The species of *Rhipidocladum* are slender and graceful. At each mid-culm node, they bear an adnate triangular flat meristematic branch that produces numerous foliage-bearing lateral branchlets in a fan-shaped (apsidate) array. The genus is differentiated vegetatively from *Merostachys,* which has a similar branchlet array, by the nature of the main culm leaves. In *Rhipidocladum,* the base of the erect culm blade is as wide as the apex of the sheath and adnate to it. In *Merostachys,* the reflexed blade of the culm leaf is pseudopetiolate and much narrower than the sheath apex.

The species of *Rhipidocladum* are slender bamboos, ranging from 2 to 10 m or more in length and 1 to 5 cm diam. They inhabit mesic sites in moist forests and are found on canyon walls and river banks at low and middle altitudes. The genus ranges from southern Mexico to northern South America, with one species reported from Brazil. McClure indicated that his genus included 11 species and offered a key to distinguish some of these. One species, *R. verticillatum,* has since been transferred to a new genus, *Actinocladum,* by Soderstrom (1981). With the addition of these three new species, the current number is 13.

Mesoamerican species of *Rhipidocladum* are not well known because of their erratic blooming cycles. Recent gregarious flowering of two Costa Rican species and one from Panama has allowed differentiation of species previously known only in the vegetative condition. Two of these species, *R. clarkiae* and *R. panamense,* are distinct from the remaining species of the genus because of their extremely large number of filiform branches. The third, *R. pacuarense,* is most closely related to *R. bartlettii* of the Petén of Guatemala and Chiapas, and their differences are stated in Table 1. In the absence of adequate type material of many of the species, detailed comparisons with the remaining species cannot be made. The key given by McClure (1973) offers the best separations to date.

Rhipidocladum clarkiae Pohl, sp. nov. TYPE: Costa Rica. Prov. San Jose: Parque Nacional Braulio Carrillo, ca. 0.6 km N of Information Booth, S of Bajo de Hondura, 1,350 m, 26 July 1982, *Pohl & Clark 14103* (holotype, ISC; isotypes, CR, K, MO, US). Figure 1a–e.

Gramen lignosum caespitosum; culmi 10–20, plus quam 10 m × 1–2 cm, cylindrati, cavi. Vaginae culmorum ca. 10 cm, glabris; laminae culmorum erectae ca. 11.5 cm × 2.5 cm, acuminatae. Ramuli floriferi 75–130 in complemento, delicati, 45–65 cm longi. Inflorescentia racemosa biseriata delicata. Spiculi 7–8, 15–30 mm longi; gluma primera acicularis, 0.5–2.5 mm, uninervia; gluma secunda ovata, 4–5.5 mm, arista ca. 3 mm; lemma sterile 4–5 mm longum anguste-ovata, 5-nervata; spiculis supra lemma sterile secedens; lemmata fertilia 2–4, 7–9 mm longa, scabrida, arista 4–6 mm; palea lemma aequans, apice scabrida; lemmata rudimentaria 2, convoluta; lodiculae 3, crystallis oxalatis obtectis.

Caespitose ligneous bamboo; culms in clumps of 10–20, more than 10 m long; internodes thin-walled, cylindrical, glabrous, 1–2 cm thick. Culm leaves with sheaths ca. 10 cm long, glabrous; ligule a stiff membrane, ca. 1 mm long, forming an inverted U-shaped line; blade as wide as the sheath apex, erect, ca. 11.5 cm by 2.5 cm, tapering gradually to an acuminate apex, appressed-hispid above near the base and margins. Flowering branches borne at many nodes, 75–130/node, unbranched, extremely thin and del-

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icate, 45–65 cm by 0.5 mm, including the inflorescences (plants not seen in vegetative phase). Branch leaves 2–3 per branch; sheaths glabrous or puberulent, the apex prolonged into an erect auricle bearing weak erect bristles to 6 mm; ligule membranous, lacerate, ciliolate; blades flat, dark green above, glaucescent beneath, 3–9 cm by 4–9 mm, the midrib very inconspicuous. Inflorescence a solitary slender unilateral raceme, terminal on the branch; peduncle scarcely exserted, puberulent; rachis 9–13 cm long, very slender, puberulent; pedicels less than 1 mm long, appressed. Spikelets 7–8 per raceme, 10–14 mm apart, erect, appressed, very slender, scarcely compressed, 15–30 mm long, disarticulating above the sterile lemma and between the fertile florets; first glume acicular, 0.5–2.5 mm long, 1-nerved, clasping the rachilla, the awn ca. 2 mm long; second glume narrowly ovate, 4–4.5 mm long, 3-nerved, the awn ca. 3 mm long; sterile lemma 4–5 mm long, narrowly ovate, 5-nerved; fertile florets 2–4, with 2 rudimentary, short-awned, convolute florets, shorter than the fertile florets and borne above, fertile lemmas 7–9 mm long, narrowly ovate, 7–9-nerved, scabrid, the awn 4–6 mm long, scabrous; paleas of fertile florets shorter than or equalling the lemmas, 2-keeled, the keels and tips scabrous; rachilla segments 4.5–6 mm long, glabrous, wrinkled, the apex coroniform; lodicules 3, thin, flat, ovate, the surface beset with numerous druses; the apex with 2–4-celled microhairs, the vascular bundles 1–2, weak, short, unbranched; anthers 3, ca. 4.5 mm long; style 1; stigmas 2; ovary beset with druse crystals.

The only known specimens of this species were collected from the same colony along the access road to the Parque Nacional Braulio Carrillo, in shade of wet broadleaf forest. The population there consisted of a number of individuals on both sides of the road. All appeared to be in bloom in 1982 and early 1983. TOPOTYPES: *Pohl 14152,* 13 Sept. 1982 (CR, F, ISC, K, MEXU, MO, US); *Davidse et al. 23228,* 23 Jan. 1983 (BM, CR, ISC, MEXU, MO, US).

This species is named for Lynn Clark, student of the genus *Chusquea,* who participated in the original collection of the species. No other collections from other colonies are known, but the species should be sought on the wet northern slopes of the Cordillera Central of Costa Rica. The plants have a delicate aspect and have ornamental possibilities.

TABLE 1. Differences between *R. bartlettii* and *R. pacuarense.*

	R. pacuarense	*R. bartlettii*
Branch leaf L/W ratio	5.6–9 : 1	15–17 : 1
Abaxial blade pubescence	base, both sides	base, one side
Rachis internodes	2–7 mm	ca. 10 mm
Spikelets/branch	22–25	6–18
Sterile lemma	7–8 mm	5–6 mm
Lemma awn length	<4 mm	0–1 mm
Anther length	2–3 mm	5 mm
Rachilla pubescence	glabrous	ultimate segment scabrous

Rhipidocladum pacuarense Pohl, sp. nov. TYPE: Costa Rica. Prov. Cartago: 1.8 km E of Río Pacuare crossing of Hwy. 232, top of hill, N side of road, 750 m, 1 Oct. 1982, *Pohl 14161* (holotype, ISC; isotypes, CR, F, K, MO, US). Figure 1f–i.

Gramen lignosum caespitosum rhizomis pachymorphis; culmi plus quam 10 m × 2–3 cm, cylindrati, cavi. Ramuli 18–30 in complemento, 20–60 cm longi. Folia ramulorum plana, 7–12 cm × 10–22 mm, subter villosa a basim. Inflorescentia racemosa biseriata, arcuata 9–17 cm × 3 mm. Spiculae angustae, 18–19 mm; gluma primera 2.5–3.5 mm, acicularis; gluma secunda 4.5–6 mm, 3–5-nervata, arista minus quam 4 mm; spiculae supra lemma sterile secedens; lemma sterile 7–8 mm longa; lemmata fertilia 3, 7–8 mm, glabra, 7–9-nervata, arista 3–4 mm; palea lemma aequans vel longior, apice hispida; lodiculae 3, vasculatae; antherae 3, 2–3 mm; stigmata 2. A *R. bartlettii* differt inflorescentia densior, aristae longiores, rachilla glabra, foliorum forma (vide Table 1).

Caespitose, ligneous bamboo; rhizomes pachymorphous; clumps small; culms more than 10 m by 2–3 cm, cylindrical, green, thin-walled, glabrous, arching and the upper portions trailing; internodes often containing liquid; nodes not prominent; supranodal ridges absent. Culm leaf sheaths 10–12 cm long; ligule a stiff membrane, 0.5–1 mm long, minutely ciliolate; blades erect, as wide as the sheath apex, the body ca. 6 cm long, with a narrow caudate apex ca. 3 cm long; margins stiffly hispid-ciliate. Branches usually 18–30 per node, 20–60 cm long, sometimes rebranched from a middle node. Branch leaves usually 3–6 per branch; sheaths glabrous, the apex truncate, bearing flexuous auricular bristles to 10 mm long; pseudopetiole smooth, purple, ca. 3

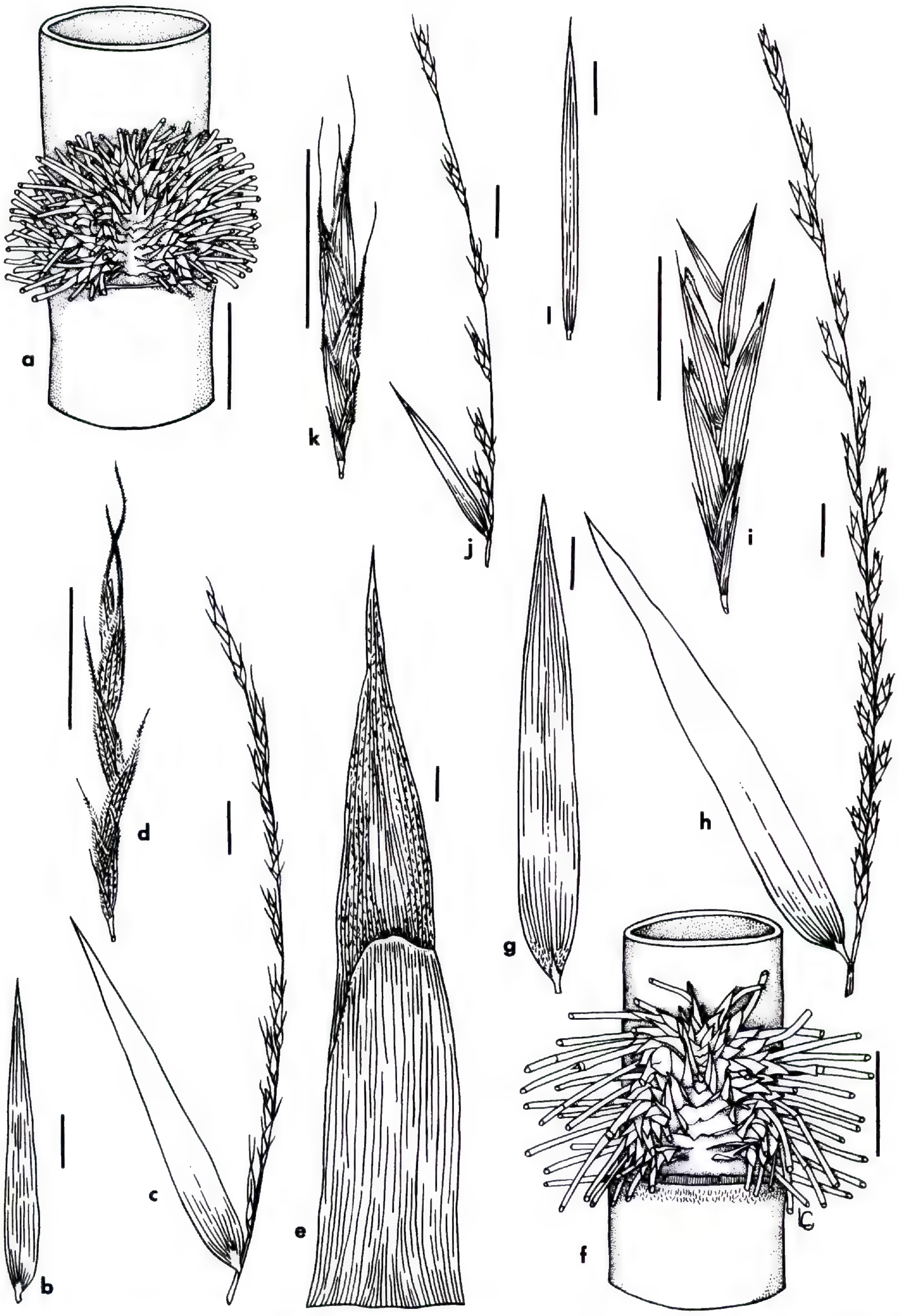

FIGURE 1. *Rhipidocladum* species. a–e. *Rhipidocladum clarkiae*.—a. Branch complement.—b. Branch leaf blade, abaxial.—c. Inflorescence.—d. Spikelet.—e. Culm leaf (all based on *Pohl & Clark 14103*). f–i. *Rhipidocladum pacuarense*.—f. Branch complement.—g. Branch leaf blade, abaxial.—h. Inflorescence.—i. Spikelet (all based on *Pohl 14161*). j–l. *Rhipidocladum panamense*.—j. Inflorescence.—k. Spikelet.—l. Leaf blade, abaxial (all based on *Gentry & Dwyer 3418*). Scale lines = 1 cm.

mm long; ligule less than 0.5 mm long; blades 7–12 mm by 10–22 mm, the length : width ratio 5.6–9 : 1, flat, without a conspicuous midrib, scabrid above, rounded to the asymmetric base, the abaxial surface glaucescent, glabrous except for patches of woolly pubescence on both sides near the base. Inflorescence a slender arcuate raceme, terminal on a primary branch or a short secondary branch from a middle node, 9–17 cm long by 3 mm wide; rachis glabrous; pedicels erect, ca. 1 mm. Spikelets 22–25 per raceme, borne 2–7 mm apart, 18–19 mm long, appressed, disarticulating above the sterile lemma and between the florets, first glume 2.5–3.5 mm long, awl-shaped, 1-nerved, tapering to an awn 3–5 mm long; second glume narrowly ovate, 4.5–6 mm long, 3–5-nerved, tapering to an awn less than 4 mm long; sterile lemma 7–8 mm long, 5–7-nerved, ciliate above, the awn 2.5–3.5 mm long; fertile florets 3; 2 reduced sterile convolute florets above; fertile lemmas 7–8 mm long, rounded on the back, 7–9-nerved, usually purplish, glabrous, stiff, awn 3–4 mm long; palea shorter or longer than the lemma, ciliate above; lodicules 3, flat, hispid at the tip; two lodicules equal, ovate, several-nerved; third lodicule shorter, lanceolate, 1-nerved; anthers 3, 2–3 mm long; style 1; stigmas 2.

Hillsides and canyons; central and southern Costa Rica; 650–1,400 m.

Representative flowering specimens. COSTA RICA. PROV. CARTAGO: valley of Río Tuís, along Hwy. 232, 2 km SE of Jicotea, 1 Oct. 1982, *Pohl 14165* (CR, F, ISC, K, MO, US).

Representative vegetative specimens. COSTA RICA. PROV. CARTAGO: *Pohl & Pinette 13182* (topotype) (ISC, MO), *Pohl & Lucas 13149* (ISC); Pavas de Turrialba, *Pohl & Pinette 13207* (ISC, MO), PROV. PUNTARENAS: Cañas Gordas, *Pohl & Pinette 13274* (ISC, MO). PROV. SAN JOSE: Río Conejo, *Pohl & Davidse 11056* (ISC, MO), *Pohl & Clark 13926* (ISC, MO); Rosario, *Pohl & Gabel 13579* (ISC). PROV. ALAJUELA: San Ramón, *Pohl & Clark 14116* (ISC).

This widespread Costa Rican bamboo differs from its closest Mesoamerican relative, *R. bartlettii* (McClure) McClure which occurs in the Petén of Guatemala and in Chiapas, in a number of respects. The most conspicuous of these are listed in Table 1. Unfortunately *R. bartlettii* is incompletely known and the type is in the flowering state only. The original description contains no information concerning the number of flowering branches per node, the culm height and diameter, or the nature of the culm leaves. The differences between the Costa Rican plants and the type of *R. bartlettii* that can be determined from available material are mostly spikelet characters, but they appear to indicate that these two populations represent distinct species, a conclusion supported by their apparent geographical disjunction.

This species occurs in scattered small populations at lower and middle elevations in moist areas of central and southern Costa Rica. I have observed various of these populations in the vegetative state at different times between 1968 and 1982. One of these colonies, *Pohl & Pinette 13207,* collected in 1976, at that time lacked new culms or culm sheaths, indicating the imminence of blooming. Specimens *13182, 13149,* and *14161* are all from the same population at the type locality east of the Río Pacuare. Blooming was first observed at this locality in 1982. The Río Tuís population, which was in bloom at the same time, was about 5 km distant from the type locality. From this collection site, we could observe massive gregarious blooming at a distance, along the Río Tuís.

Canes of this species arch and droop, the upper portions trailing on the soil. The culms are very thin-walled and break with a loud "pop." Some young internodes contained liquid. The plants are graceful and have potential as an ornamental.

Rhipidocladum panamense Pohl, sp. nov. TYPE: Panama. Prov. Panamá: 1–2 mi. beyond Goofy Lake, 1 Jan. 1972, *Gentry & Dwyer 3418* (holotype, ISC; isotype, MO). Figure 1j–l.

Gramen lignosum; culmi scandentes, ad 5 m longa, cylindrati, cavi, 5–7 mm diam. Ramuli floriferi supra 200 in quoque nodum, ad 35 cm longi; folia ramulorum 2–4, plana, 3–6 cm × 2–3 mm, linearia. Inflorescentia racemosa unilateralis, tenuis. Spiculae 5–7, 12–16 mm longae; gluma primera 2.5–3.5 mm longa; secunda 4–7 mm, 5-nervata, arista 3–4.5 mm longa; lemmata fertilia 2, 5.5–6 mm, 7–9-nervata, arista 3–6 mm longa; lemma dorsalis hispidula; flosculi rudimentarii 2–3. A *R. clarkiae* recedit foliis tenuiores, spiculis breviores, et rami supra 200 in complemento.

Ligneous bamboo; culms clambering, to 5 m long, the basal diameter unknown; flowering internodes hollow, cylindrical, glabrous, 5–7 mm thick; branches 200–230 per node, very slender, to 35 cm long, including inflorescences; nodes swollen. Branch leaves 2–4 per branch; sheaths glabrous or sparsely puberulent; auricular bristles sparse or absent, ca. 2 mm long; ligule obsolete; blades 3–6 cm by 2–3 mm, linear, tapered to the pseudopetiole, glabrous or sparsely his-

pidulous above, glabrous or puberulent beneath; 1 strong nerve near one margin. Inflorescence a very slender unilateral raceme, 4–12 cm long, terminal on a leafy primary branch or a short secondary branch arising from a middle node. Spikelets 5–7 per raceme, appressed, borne 5–20 mm apart, 12–16 mm long, very slender, scarcely compressed, disarticulating above the sterile lemma and between the fertile florets; first glume 2.5–3.5 mm long, narrowly ovate, awnless; second glume 1-nerved, 4–7 mm long, clasping, 5-nerved, the awn 3.5–4.5 mm long; sterile lemma narrowly ovate, 5.5 mm long, 7-nerved, the awn 3–4 mm long; fertile florets 2, with 2–3 rudimentary, convolute florets above; fertile lemmas narrowly ovate, 5.5–6 mm long, 7–9-nerved, the awn 3–6 mm long, the back hispidulous along the margins and near the apex; paleas of fertile lemmas longer or shorter than the lemma, ciliate at the apex; anthers not seen; style 1; stigmas 2.

Forests, provinces of Darién and Panamá, Panama. This species is similar to *R. clarkiae*, both having large numbers of branches at the flowering nodes, which separates them from all other known species of *Rhipidocladum*. *Rhipidocladum panamense* differs from *R. clarkiae* in the much narrower and shorter leaf blades, smaller spikelets, and the much larger number of flowering branchlets.

Representative flowering specimens. PANAMA. PROV. PANAMÁ: Goofy Lake, 16 Aug. 1967, *Dwyer & Hayden 8037* (MO); 2 mi. above Goofy Lake, 16 Aug. 1967, *Stimson 5377* (MO); 7 mi. N of Cerro Azul, road to Cerro Jefe, 2,600 ft., 13 Nov. 1965, *Blum, Godfrey & Tyson 1810* (MO); Cerro Azul, 2,000 ft., 3 Nov. 1965, *Tyson 2116* (MO).

Nee 10711 (ISC, MO) from the Río San Felix, Chiriqui, is similar to the preceding, but has much longer, awnless lemmas. Until specimens with intact spikelets can be obtained, I cannot place it.

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SYSTEMATICS OF THE SOUTHERN AFRICAN GENUS *GEISSORHIZA* (IRIDACEAE—IXIOIDEAE)[1]

PETER GOLDBLATT[2]

ABSTRACT

Geissorhiza is a large genus of small, corm bearing perennials endemic in the Cape Province of South Africa and is restricted to the winter rainfall area of the south and west coasts and immediate interior. The genus is defined by its asymmetric corms with hard, often woody tunics, herbaceous bracts, and long style with short recurved branches. It is separated by style morphology from the closely related *Hesperantha,* in which the style is included in the perianth tube and the style branches are long and spreading, and, in addition, the anthers of *Hesperantha* are introrse at anthesis. Eighty-one species are recognized in this study, 29 described here for the first time. This represents an increase of some 25 over the 52 species of true *Geissorhiza* admitted by Foster (1941) in his revision of the genus and the eight species placed by Lewis (1941) in *Engysiphon,* a genus here reduced to synonymy. A novel subgeneric classification is proposed in which two subgenera, *Geissorhiza* (34 spp.) and *Weihea* (47 spp.) are recognized, each including several sections. *Geissorhiza* is seen as a late Tertiary genus that probably differentiated in upland southeastern Africa when much of southern Africa including the Cape Region was still heavily forested. The continuing deterioration of the climate in the Pliocene and Pleistocene that culminated in the establishment of a Mediterranean climate in the southwestern Cape probably gave the impetus to the extensive radiation in the mountains and western coastal belt in this area, where most species, including all of the more specialized taxa, occur. Primitive taxa are concentrated along the relatively well-watered southern Cape coast, where little speciation has occurred and the primitive taxa appear to have differentiated slowly by a process of phyletic evolution. The geography of *Geissorhiza* is analyzed in detail and several important centers of endemism, corresponding closely with Weimarck's phytogeographical subdivisions are identified. The major trends in the evolution of *Geissorhiza* include: the development of imbricate corm tunics from the basic concentric type; the reduction or extreme elongation of the perianth tube; the development of floral zygomorphy; and the elaboration of the leaf lamina, which may become several ribbed and grooved (section *Geissorhiza*), or may have raised and winged ciliate margins and a winged midrib (section *Ciliata*) or thickened margins and midrib (especially sections *Angustifolia* and *Ixiopsis*). Cytological studies have brought the number of species in which the chromosome number is known to 41, over half the genus. Basic chromosome number is $x = 13$, and while most species are diploid, polyploidy has been recorded in a few species including the triploid vegetative apomict, *G. bolusii.* The conservation status of *Geissorhiza* is reviewed and several seriously threatened species are identified including almost all those endemic to the coastal plain between Cape Town and Piketberg, an intensively farmed area rich in species.

Geissorhiza is a large genus of medium to small, corm bearing plants, restricted entirely to the winter rainfall region of the south and west coasts of southern Africa. It is centered in the mountains and western coastal belt of the southwestern Cape, with species extending as far east as Grahamstown in the eastern Cape and as far north as Steinkopf in northern Namaqualand. *Geissorhiza* is a member of Ixioideae, a predominantly African subfamily, strongly developed in southern Africa, and is distinguished by its woody to papery (rarely fibrous) corm tunics, asymmetric corms, herbaceous floral bracts, and long, exserted style (included in two species) with short recurved style branches. It is most closely related to *Hesperantha* (ca. 55 spp.—Goldblatt, 1982a,

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ANN. MISSOURI BOT. GARD. 72: 277–447. 1985.

1984) from which it differs mainly in its style and style branches. In addition, *Hesperantha* is unusual in the family in having introrse anthers at anthesis.

Since its treatment in "Flora Capensis" (Baker, 1896) in which 29 species were recognized, *Geissorhiza* has been completely revised only by Foster (1941). Foster admitted 55 species to the genus, three subsequently transferred to *Gladiolus,* including the only species he recognized from Madagascar, *G. bojeri* (Goldblatt, 1982b). A second Madagascan species *Geissorhiza ambongensis,* which he regarded as "doubtful or unknown," is here also excluded from *Geissorhiza* but its correct generic position is uncertain. Despite having been revised relatively recently, *Geissorhiza* has, for reasons outlined below, been poorly understood. Foster's revision was based on herbarium material only but he did not examine the important collections in South African herbaria, and was thus unaware of several undescribed species in these collections. The revision was also in part unnatural, combining unrelated taxa in some subsections, and the key was difficult to use. In addition, extensive collecting in South Africa, especially in recent years, has resulted in the discovery of many species that were clearly undescribed. A few of these are local lowland endemics but most are montane species of middle and upper elevations, many discovered only in the last 40 years, as the Cape mountain flora was systematically explored, largely by the Cape botanist, Elsie Esterhuysen.

Eighty-one species in two subgenera and 12 sections are recognized in this treatment (Table 1), in which *Engysiphon* Lewis (8 spp.) is reduced to sectional rank. Some 12 species admitted by Foster are reduced to synonymy, two to subspecies status, while two of Foster's varieties are raised to specific rank, and 29 species are described here for the first time. The subgeneric classification followed here is novel, being based primarily on the characteristics of the corm rather than the leaf which were considered of more fundamental importance by Foster. Both corm and leaf structure vary to an unusual extent in *Geissorhiza* and these aspects are examined in detail in this study. Chromosome cytology, also investigated here, is relatively uniform with $x = 13$ the basic chromosome number. Most of the 40 species known cytologically are diploid, but *G. bolusii* is an apomictic triploid, and three species are tetraploid, or have tetraploid races.

RELATIONSHIPS AND SYSTEMATIC POSITION OF *GEISSORHIZA*

Geissorhiza is a member of the largely African subfamily Ixioideae, an alliance defined by a spicate inflorescence, the sessile flowers of which are subtended by a pair of opposed bracts. The tepals are always united in a tube which is often well developed, and the rootstock is a basally rooting corm that typically has a stele (De Vos, 1977).

It is reasonably well established on morphological and cytological grounds (Lewis, 1954; Goldblatt, 1971, 1982a, 1984) that *Geissorhiza* is most closely related to *Hesperantha,* a widespread African genus of some 55 species, also centered in the southern African winter rainfall region. The apparently primitive species of both genera have identical asymmetric corms with light brown, firm to woody, concentric tunics, herbaceous floral bracts, small actinomorphic flowers, and membranous capsules with numerous turbinate to angular seeds. Unspecialized species of both genera can in fact only be distinguished by their different style and style branches and anther dehiscence in the actinomorphic flowered species. In *Geissorhiza,* the long style is well-exserted from the perianth tube and divides towards the apex of the anthers into three short recurved branches (near the base of the anthers in three species and the style included in two more). *Hesperantha* differs in having a relatively short style, typically dividing in the throat of the perianth tube into three long laxly spreading branches. The anthers of *Hesperantha* are introrse at anthesis, contrary to the normal condition for species of Iridaceae with actinomorphic flowers.

The two genera share a common basic chromosome number, $x = 13$, a number unusual in Iridaceae, but also found in the related *Schizostylis* (mono- or di-typic) and in some species of the apparently unrelated *Romulea* (De Vos, 1972). Lewis (1954) placed *Geissorhiza* in a sub-

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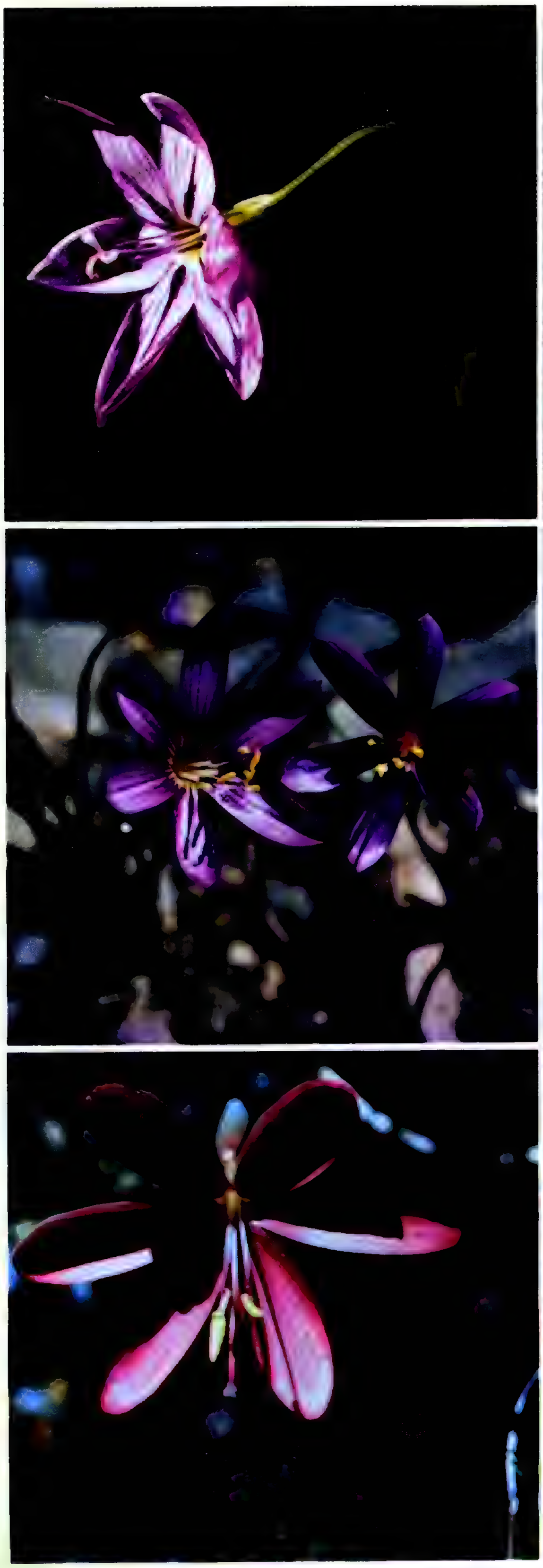
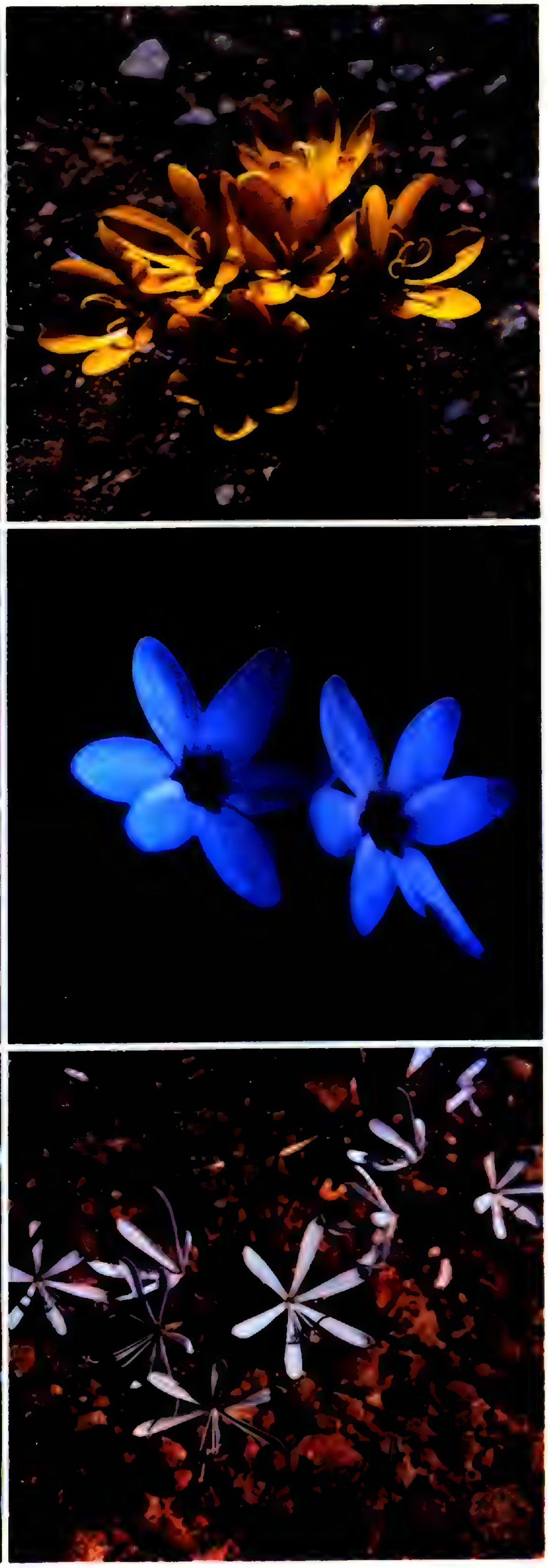
FIGURES 1–6. From left to right and top to bottom.—1. *Geissorhiza elsiae.*—2. *G. corrugata.*—3. *G. karooica.*—4. *G. cedarmontana.*—5. *G. nubigena.*—6. *G. longifolia.*





tribe Ixiinae close to *Hesperantha* in a lineage that also includes *Gladiolus* and the small, highly specialized genera such as *Homoglossum* and *Anomalesia,* closely allied to *Gladiolus.* In a more refined classification (Goldblatt, 1971), *Geissorhiza* is placed together with *Hesperantha, Schizostylis,* and the monotypic *Melasphaerula* in Hesperanthinae, a classification that still seems to best reflect the relationships of these genera. *Melasphaerula* ($x = 11$) is probably isolated in the alliance, if it correctly belongs here, but it has the woody corm tunics that define the subtribe.

The difference between *Geissorhiza* and *Hesperantha* appears to be based on relatively minor features but nevertheless, they appear on phenetic grounds to comprise monophyletic assemblages. The patterns of variation are coherent in both genera and are consistent with the contention that they are indeed natural groups, even though *Geissorhiza* can at present only be defined negatively, with respect to *Hesperantha,* by a combination of unspecialized characteristics.

The unspecialized species of *Hesperantha* have pale, white or pink flowers and are usually evening blooming and strongly sweet scented. The genus is believed to be a basically moth pollinated group but day blooming species with colored flowers are probably bee pollinated (Vogel, 1954; Goldblatt, 1984). In contrast, the species of *Geissorhiza* are always day blooming and typically scentless, and the genus is believed to be largely bee pollinated (Vogel, 1954).

MORPHOLOGY OF *GEISSORHIZA*

Species of *Geissorhiza* are small, geophytic corm bearing perennials. Actual age is difficult to determine but plants with up to 12 annually produced corm tunic layers are known. With the exception of *G. outeniquensis,* species grow actively in the wet seasons of the year, usually winter and spring (or summer at higher altitudes), flower in spring or summer, and become dormant during the dry, later spring or summer and autumn. *Geissorhiza outeniquensis* is apparently evergreen and has a very reduced underground storage organ. It grows in permanently moist montane habitats and appears to have no dormant period during the year. *Geissorhiza fourcadei* flowers in the autumn but it is restricted to sites that remain moist throughout the summer or all year.

All parts of the plant body have some specialized features and these are discussed in the following pages, under the main headings of corm, leaves, stem, inflorescence, flower, stamens, gynoecium, and fruit.

CORM

The corm of *Geissorhiza* consists of a swollen internode with an apical bud, typically covered with hard, woody to firm and papery tunics. The live portion of the corm is a white (Fig. 13A–E) asymmetric body, being somewhat flattened on one side or towards the base, and with a peculiar downward oriented projection at the lower end of the flattened side, from which the roots are produced. The corms vary considerably in the genus but fall into two main groups, those with concentric or with imbricate tunics (the terminology of Foster, 1941, 1948).

The basic tunic type is assumed to be one with concentric layers, a type shared with the related genus *Hesperantha,* in which corm and tunic morphology have recently been described in detail (Goldblatt, 1982b). Here the overall shape is often asymmetric (Fig. 13), reflecting the internal structure but the presence of the lateral projection is not always evident externally. Corms with concentric tunics are usually small, of constant size, and the older tunic layers split irregularly from base and apex into somewhat elliptic sections which completely enclose the new tunic layers produced in successive years. The tunics are usually light to middle brown in color.

In the second major corm type in *Geissorhiza,* the outer tunics cover the inner above only, and are thus imbricate. The corm shape is usually nearly symmetric and more or less ovoid with a small flat basal part. The tunics are usually dark brown to blackish, but in *G. similis* and *G. scillaris* they are a light brown color as in species with concentric corm tunics. In either case, the layers are notched below in a regular pattern that gives the corms their very characteristic appearance (Fig. 13F–K). The upward displacement of

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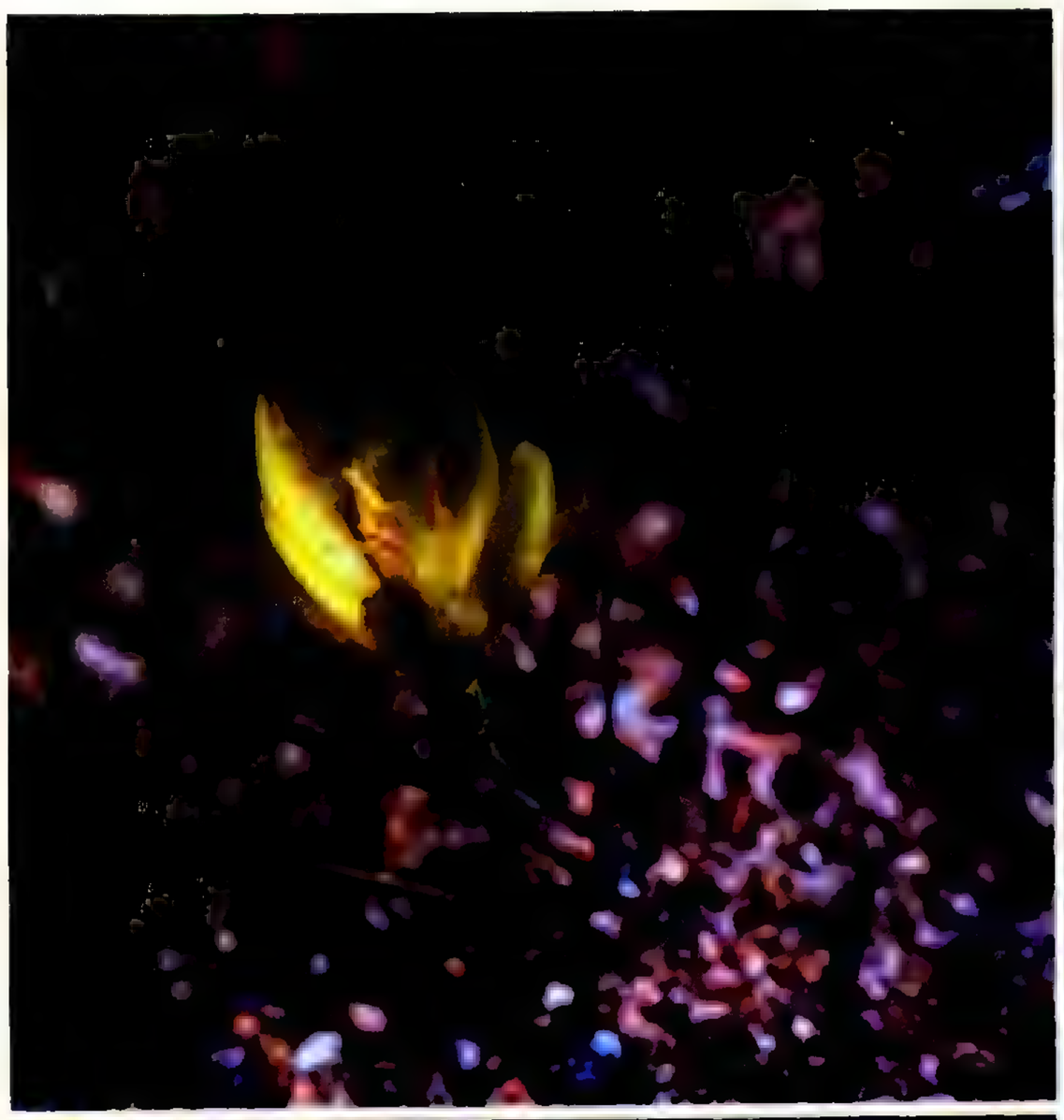
FIGURE 7–12. From left to right and top to bottom.—7. *Geissorhiza malmesburiensis.*—8. *G. barkerae.*—9. *G. purpureolutea.*—10. *G. mathewsii.*—11. *G. radians.*—12. *G. splendidissima.*



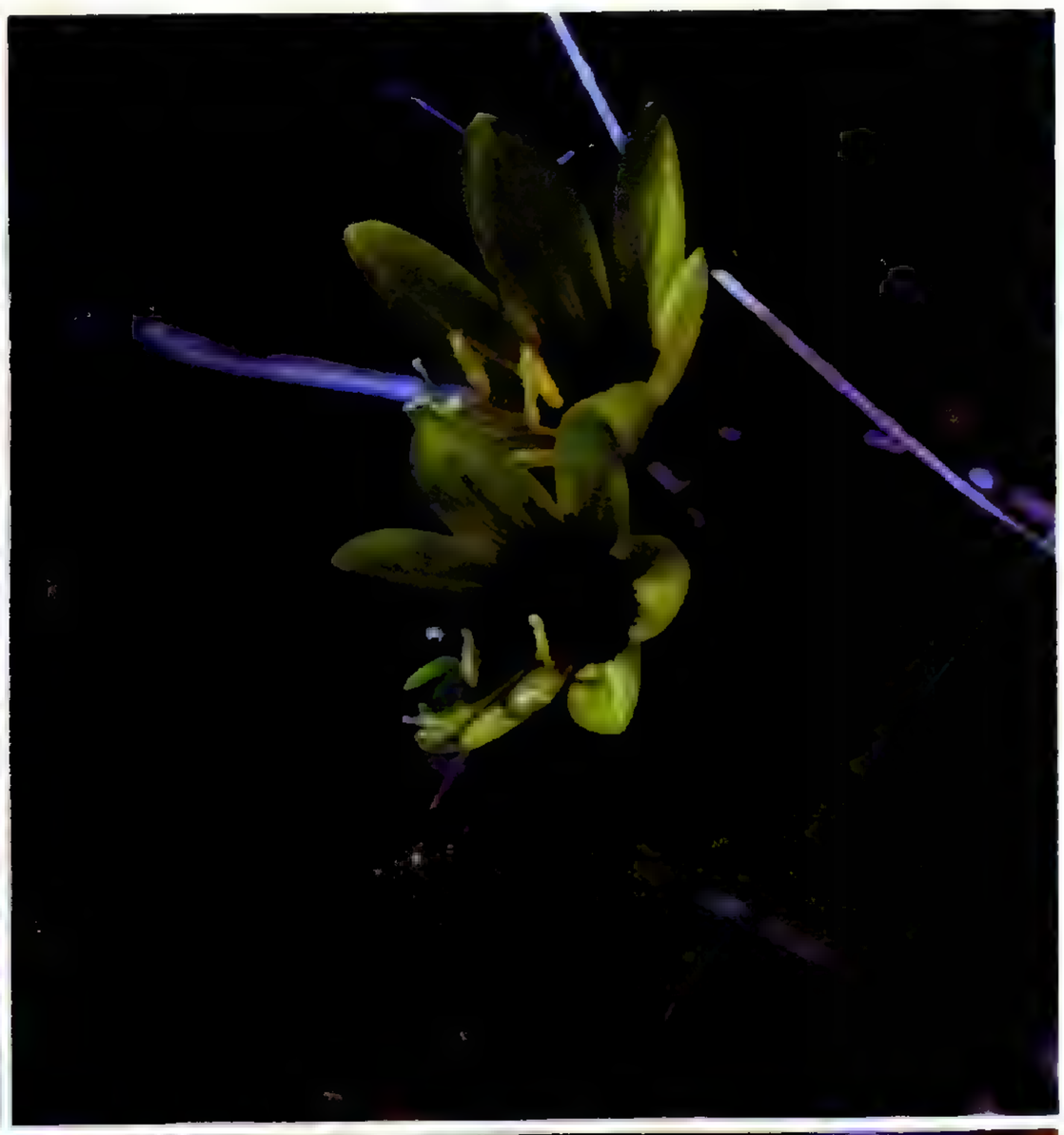


TABLE 1. The species of *Geissorhiza* arranged in systematic order, in their sections. Brief distribution and habitat data are also listed for convenience.

Subgenus *Weihea* (Baker) Goldbl.	
Section *Weihea*—18 spp.	
1. *G. inconspicua* Baker	S Cape between Swellendam and Uitenhage
2. *G. elsiae* Goldbl.	Kammanassie Mts.
3. *G. roseoalba* (Lewis) Goldbl.	Little Karoo, Longkloof to Uitenhage
4. *G. outeniquensis* Goldbl.	wet shady sites, Outeniqua Mts., George district
5. *G. fourcadei* (L. Bolus) Lewis	Swartberg, Outeniqua and Tsitsikamma Mts., Robinsons Pass to Humansdorp
6. *G. foliosa* Klatt	slopes flats at the foot of the Langeberg
7. *G. nigromontana* Goldbl.	Great Swartberg, along streams
8. *G. delicatula* Goldbl.	mts. of the interior S Cape
9. *G. bracteata* Klatt	S Cape near Albertinia to E Cape at Grahamstown
10. *G. nana* Klatt	Caledon district to Riversdale, clay slopes and flats
11. *G. setacea* (Thunb.) Ker	SW Cape, wet sandy flats
12. *G. ornithogaloides* Klatt subsp. *marlothii* (Foster) Goldbl.	widespread in the interior Cape region, Cedarberg E to the Long Kloof
subsp. *ornithogaloides*	Paarl district to Caledon and Bredasdorp
13. *G. malmesburiensis* Foster	Malmesbury, sandy slopes
14. *G. geminata* E. Meyer ex Baker	wet sites, interior SW Cape
15. *G. ovalifolia* Foster	damp sites, SW Cape mts.
16. *G. bolusii* Baker	damp shady sites, SW and W Cape mts.
17. *G. parva* Baker	SW and W Cape mts., sandy soils and rocks
18. *G. ovata* (Burm.f.) Asch. & Graeb.	SW and S Cape, sandy soils, mainly montane
Section *Tortuosa* Foster—3 spp.	
19. *G. corrugata* Klatt	Calvinia district, shale flats
20. *G. spiralis* (Burch) De Vos ex Goldbl.	Sutherland district, W Karoo flats
21. *G. karooica* Goldbl.	Matjesfontein Karoo, S-facing shale slopes
Section *Pusilla* Goldbl.—1 sp.	
22. *G. pusilla* (Andr.) Klatt	damp shady places, Peninsula and surrounding hills
Section *Includanthera* Goldbl.—2 spp.	
23. *G. esterhuyseniae* Goldbl.	Great Winterhoek Mts., rocky S slopes at 2,000 m
24. *G. cedarmontana* Goldbl.	Central Cedarberg above 1,200 m, steep S slopes
Section *Angustifolia* Goldbl.—11 spp.	
25. *G. lithicola* Goldbl.	lower slopes of the Kogelberg Mts., in rocky ground
26. *G. purpurascens* Goldbl.	SW Cape, sandy flats at isolated sites between Stellenbosch and Piketberg
27. *G. humilis* (Thunb.) Ker	sandy flat places, Cape Peninsula and Flats
28. *G. darlingensis* Goldbl.	local in damp flats around Darling
29. *G. hispidula* (Foster) Goldbl.	sandy flats and slopes, Peninsula to Albertinia
30. *G. pappei* Baker	rare, sandy mt. soils, SW Cape
31. *G. intermedia* Goldbl.	rare, mts. between Simonsberg and Porterville
32. *G. unifolia* Goldbl.	high elevations in the Cedarberg
33. *G. juncea* (Link) A. Dietr.	sandy flats and slopes, Caledon to Pakhuis Pass
34. *G. furva* Ker ex Baker	SW Cape, stony lowlands between Paarl and Gouda
35. *G. stenosiphon* Goldbl.	Hexberg, Cold Bokkeveld Mts.
Section *Ixiopsis* Goldbl.—5 spp.	
36. *G. umbrosa* Lewis	mid to upper elevations, Peninsula and Hottentots Holland to the Cedarberg
37. *G. alticola* Goldbl.	higher peaks, Bains Kloof to Wemmershoek
38. *G. hesperanthoides* Schltr.	damp and marshy slopes, Bains Kloof to Bredasdorp
39. *G. cataractarum* Goldbl.	waterfalls and damp cliffs, Bettys Bay to Hermanus
40. *G. nubigena* Goldbl.	higher mts., Gt. Winterhoek to Kogelberg Mts.

TABLE 1. Continued.

Section *Engysiphon* (Lewis) Goldbl.—7 spp.	
41. *G. brevituba* (Lewis) Goldbl.	Piketberg Mts.
42. *G. schinzii* (Baker) Goldbl.	mts. of the Caledon district
43. *G. longifolia* (Lewis) Goldbl.	stony often shale soils, Michells Pass to Gifberg
44. *G. confusa* Goldbl.	stony mountain soils, French Hoek to Gifberg
45. *G. bonae-spei* Goldbl.	S Cape Peninsula
46. *G. tenella* Goldbl.	sandy flats and dunes, Darling to Bredasdorp
47. *G. exscapa* (Thunb.) Goldbl.	sandy flats and plateaus, Blouberg to Hondeklipbaai
Subgenus *Geissorhiza*	
Section *Intermedia* Goldbl.—2 spp.	
48. *G. similis* Goldbl.	sandy slopes and flats, Cape Peninsula to Bains Kloof
49. *G. scillaris* A. Dietr.	sandy slopes and plateaus, Caledon to the Cedarberg
Section *Geissorhiza*—10 spp.	
50. *G. imbricata* (de la Roche) Ker	
subsp. *imbricata*	Cape Peninsula to Bredasdorp
subsp. *bicolor* (Thunb.) Goldbl.	W Cape, wet sandy flats
51. *G. purpureolutea* Baker	W Cape coastal belt, wet flats
52. *G. barkerae* Goldbl.	wet marshy sites at foot of the Piketberg
53. *G. louisabolusiae* Foster	Olifants River Valley around Citrusdal
54. *G. brehmii* Eckl. ex Klatt	seasonal pools in the SW Cape
55. *G. sulphurascens* Foster	wet sandy soils, Nieuwoudtville Escarpment
56. *G. minuta* Goldbl.	rare in wet sites in the Pakhuis Mts.
57. *G. eurystigma* L. Bolus	rare, Darling to Kalabaskraal
58. *G. mathewsii* L. Bolus	rare, around Darling, vlei margins
59. *G. radians* (Thunb.) Goldbl.	damp sites, SW Cape from Gordons Bay to Saldanha
Section *Monticola* Goldbl.—8 spp.	
60. *G. burchellii* Foster	middle elevations, Bains, Kloof to the Langeberg
61. *G. grandiflora* Goldbl.	mts. among rocks, Gt. Winterhoek to the Langeberg
62. *G. tabularis* Goldbl.	semi marshy places, Table Mt., Cape Peninsula
63. *G. ramosa* Ker ex Klatt	mt. slopes, Hermanus to Tulbagh
64. *G. bryicola* Goldbl.	waterfalls and stream edges, Hermanus Mts.
65. *G. scopulosa* Goldbl.	high altitudes, Hex River Mts.
66. *G. ciliatula* Goldbl.	high altitudes, Cedarberg
67. *G. pseudinaequalis* Goldbl.	damp mt. slopes and cliffs, Ceres to Stellenbosch
Section *Planifolia* Goldbl.—4 spp.	
68. *G. aspera* Goldbl.	sandy flats and slopes, W Cape
69. *G. inaequalis* L. Bolus	W Cape mts., Bains Kloof to Nieuwoudtville
70. *G. monanthos* Eckl.	W Cape coast, often on granite outcrops
71. *G. tulbaghensis* F. Bolus	clay flats, Tulbagh
Section *Ciliata* Goldbl.—10 spp.	
72. *G. namaquensis* Barker	Namaqualand, Kamiesberg to S Richtersveld
73. *G. kamiesmontana* Goldbl.	local in the Kamiesberg above 4,000 ft.
74. *G. divaricata* Goldbl.	Nieuwoudtville Escarpment and Gifberg
75. *G. subrigida* L. Bolus	Nieuwoudtville Escarpment
76. *G. heterostyla* L. Bolus	widespread, S Cape to Worcester and N through the Roggeveld to S Namaqualand
77. *G. arenicola* Goldbl.	Nieuwoudtville Escarpment and Gifberg
78. *G. splendidissima* Diels	near Nieuwoudtville
79. *G. inflexa* (de la Roche) Ker	SW Cape, Bredasdorp to Piketberg, shale slopes and flats
80. *G. erubescens* Goldbl.	Pakhuis Pass, shale slopes
81. *G. leipoldtii* Foster	Clanwilliam to Bidouw valley, shale soils

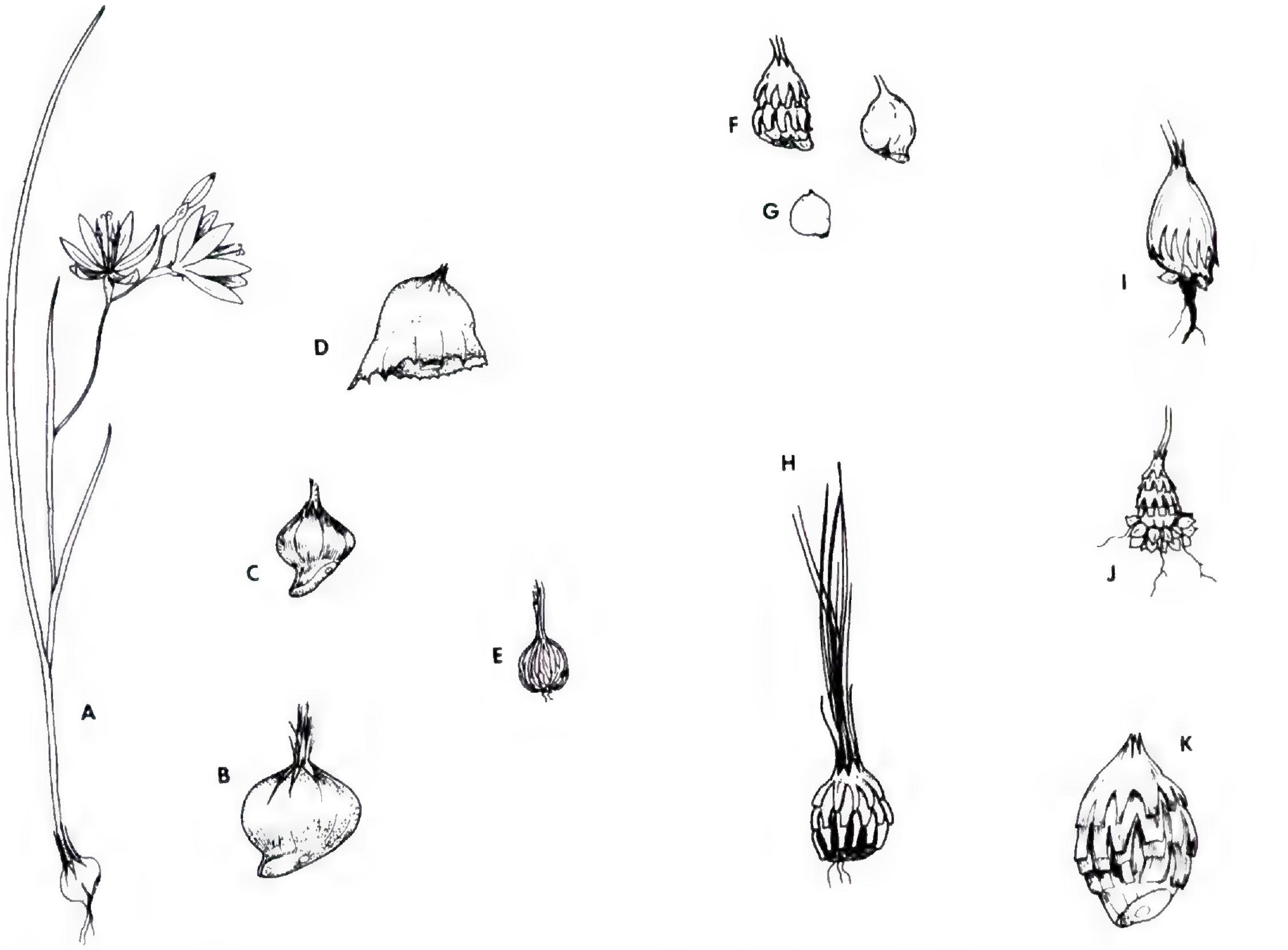


FIGURE 13. Corm morphology in *Geissorhiza*. A–E. Subgenus *Weihea*. F–K. Subgenus *Geissorhiza*.—A. *G. furva*.—B. *G. ovata*.—C. *G. juncea*.—D. *G. ornithogaloides* subsp. *ornithogaloides*.—E. *G. hesperanthoides*.—F, G. *G. inflexa* with tunic layers progressively removed and G. the naked corm.—H. *G. scillaris*.—I. *G. grandiflora*.—J. *G. monanthos* with numerous cormlets around the base.—K. *G. aspera* (all more or less life size except A, ×0.5).

the older tunics is usually easy to recognize, but occasionally the displacement is minimal and the corm type can be difficult to determine.

The difference in the corm types in *Geissorhiza* is so marked and is correlated with other important features in that it is considered a fundamental character in the genus and the basis for the recognition of subgenera. Species with concentric tunics are assigned to subgenus *Weihea* while those with imbricate tunics fall in subgenus *Geissorhiza*.

In both subgenera, species growing in perennially moist to wet habitats tend to have much softer textured tunics, and this is believed to be a secondary development. This occurs in other genera with typically hard corm coverings and cannot be considered significant above the species or sectional rank. This condition is most extreme in *Geissorhiza outeniquensis*, and *G. cataractarum*, species that grow close to permanent water. The corm coverings of *G. hesperanthoides*, *G. nubigena*, and some forms of *G. umbrosa* are most unusual in being composed of reticulate fibers. The relatives of these closely allied species have soft textured, concentric tunics, and they are clearly members of subgenus *Weihea*.

In subgenus *Weihea*, the corms of section *Engysiphon* are unusually large and the tunics particularly hard and persistent so that species of this group can often be recognized from their corms alone. In this subgenus, the corms of *Geissorhiza ornithogaloides* subsp. *ornithogaloides* and *G. malmesburiensis* are also distinctive (Fig. 13) in having a broad, oblique to horizontal base, and the tunic layers are serrated below.

In subgenus *Geissorhiza*, the corms are uniform in sections *Geissorhiza*, *Planifolia*, and *Ciliata*, being hard, woody, and dark colored. In section *Monticola*, the tunics tend to be softer and less persistent, possibly reflecting their montane and less extreme habitat. The pale tunics of *G. similis* and *G. scillaris*, assigned to section

Intermedia, have already been mentioned. It is not clear whether the corms of these two species represent a convergent development or are simply a variation or modification of the basic imbricate type of subgenus *Geissorhiza*. In the absence of further information, it is regarded as the latter and accordingly the section is included in this subgenus.

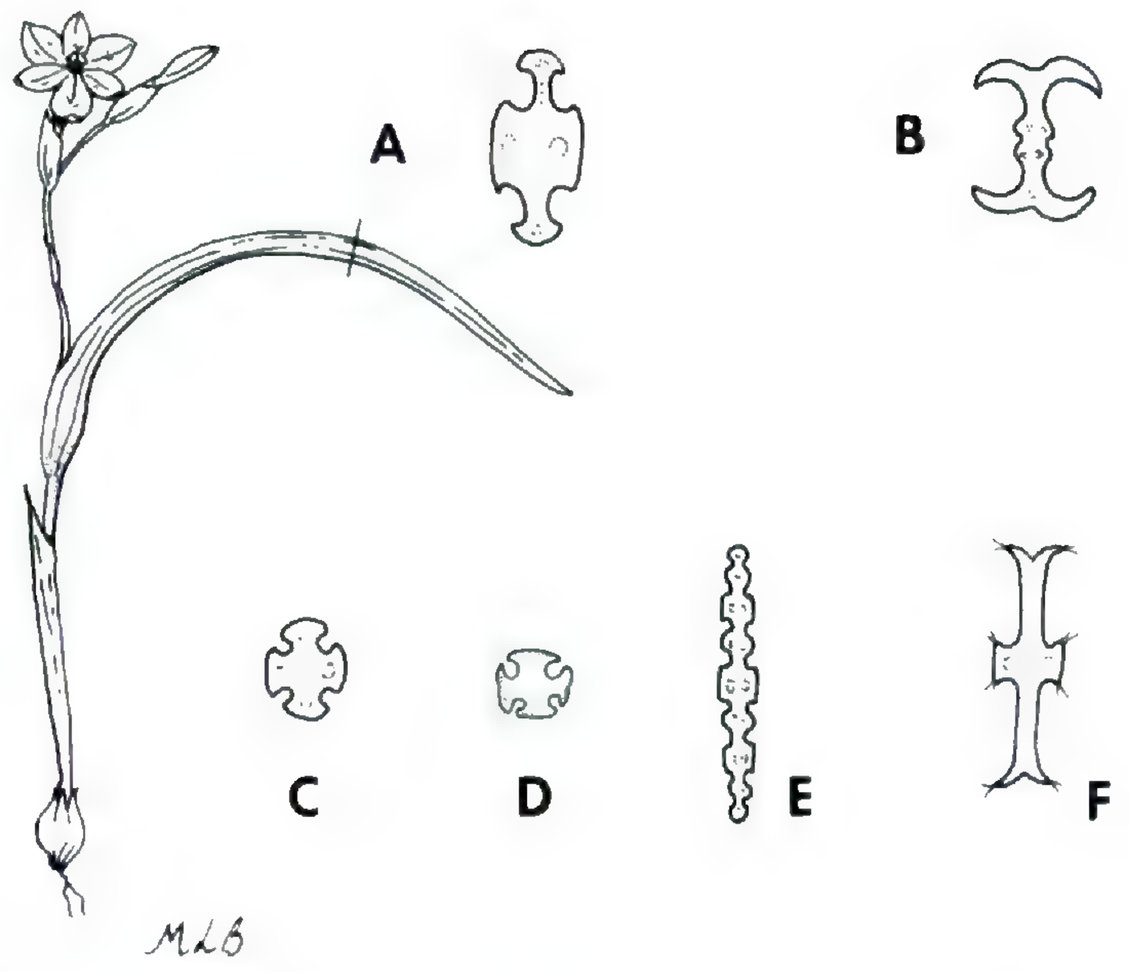


FIGURE 14. Leaf morphology of *Geissorhiza*.—A. *Geissorhiza unifolia* with enlarged transverse section showing the raised midrib area and margins.—B. *G. bonae-spei*, margins winged but midrib not thickened.—C. *G. scillaris*, heavily thickened margins and midrib.—D. *G. juncea*, terete 4-grooved leaf.—E. *G. imbricata*, ribbed leaf.—F. *G. leipoldtii*, leaf margin wings and edges of raised midrib ciliate (whole plant life size; leaf sections much enlarged).

LEAVES

Cataphyll. There is usually a single transparent and membranous cataphyll sheathing the stem base below ground. It is often lacking or fragmentary in dry material and seldom distinctive. Occasionally, the cataphyll is firm textured, persistent and brown, and forms a characteristic feature of species like *Geissorhiza erubescens, G. divaricata, G. parva,* and *G. ovata.*

Foliage leaves. These are defined as having a free, monofacial apex as opposed to stem bracts which are entirely sheathing. There may be from several to only three, less often two, and one only in *Geissorhiza unifolia.* The leaf number in most species is constant. The primitive state is presumed to be several and indeterminate as in *G. foliosa, G. bracteata,* and *G. inconspicua* (all section *Weihea*). Leaf number has stabilized at three in many species of both subgenera, where the most frequently encountered condition is two basal or nearly basal and long leaves and a third cauline and shorter, partly sheathing leaf. This uppermost leaf occasionally has a somewhat inflated and spathe-like sheath, or it may be reduced and entirely sheathing in which case it is regarded as a bract rather than a leaf. In *G. scillaris* only two leaves are produced, the lower with a long free lamina and the upper also long but sheathing for almost its entire length.

The basic leaf type in the genus, as for Iridaceae in general, is ensiform and equitant with a plane lamina in which the margins and the midrib can be readily distinguished but are not substantially thickened or raised. This basic leaf ground plan has been more extensively modified in *Geissorhiza* than in any other genus of the family with the possible exception of *Gladiolus* (Fig. 14).

The simplest modification is a narrowing from ensiform to linear, a common feature of species in the most primitive section *Weihea.* Among the species with plane leaves, *G. pusilla* stands out in having partly pubescent leaves. The species is unusual in several ways and has been assigned to its own section, *Pusilla.* Unusual broad, often ovate and prostrate or nearly prostrate leaves are found in *G. ovata* and sometimes *G. parva.*

A more complex development is a thickening of the margins and the midrib so that the leaves become distinctly 2-channelled on each surface (Fig. 14A, C), and the edges of the thickened margins are sometimes minutely ciliate. Leaves of this type occur in some species of subgenus *Weihea,* in sections *Angustifolia, Ixiopsis,* and *Engysiphon* as well as in subgenus *Geissorhiza.* In *G. exscapus, G. tenella,* and *G. bonae-spei* of section *Engysiphon,* the margins are raised, forming wings held at right angles to the blade while the midrib is hardly raised at all. These leaves are thus H-shaped in cross section (Fig. 14B).

A narrowing of the blade is evident in *Geissorhiza humilis* and *G. hispidula,* and in both these species the leaves are sticky so that soil adheres to the lamina even when dry. With the contraction of the blade width, the longitudinal channels become narrowed to thin grooves. Such leaves are found in section *Ixiopsis* of subgenus *Weihea* and occasionally in species of other sections, notably *G. radians* and *G. sulphurascens* of section *Geissorhiza.* In a few species, e.g., *G. juncea, G. furva, G. brehmii, G. louisabolusiae, G. stenosiphon,* and *G. fourcadei,* the blade is

terete (Fig. 14D), but the narrow grooves, indicating their ancestry, are preserved and can be seen in cross section or even in intact leaves under the dissecting microscope.

In subgenus *Geissorhiza*, the leaves of species in section *Ciliata* are distinctive in having the margins extended to form wings held at right angles to the blade (Fig. 14F), the midrib also raised and winged, and their edges are ciliate to pubescent. In *G. subrigida*, and robust forms of *G. inflexa*, *G. divaricata*, and sometimes other species of the section, secondary veins may also be raised and ciliate.

The leaves of most species of section *Geissorhiza* are unusual in having several veins as well as the margins heavily thickened so that the blade is several ribbed and grooved (Fig. 14E). The sheathing part of the third and uppermost leaf in this alliance is inflated and also heavily ribbed and grooved, and this character is preserved even when the lamina has become narrow and only 2-grooved (*G. radians*, *G. sulphurascens*, forms of *G. imbricata*) or terete (*G. brehmii*, forms of *G. louisabolusiae*).

Bract leaves. These appear to be modified upper leaves in which the free part of the lamina has been suppressed. They range from green and leaf-like, but entirely sheathing, to membranous and even scale-like. The presence of a bract leaf is typically constant for a species and is present even when the stem is unbranched. Such bracts are a diagnostic feature of *G. scillaris*, *G. heterostyla*, and all species of section *Monticola*.

STEM

The stem is typically erect, smooth, terete, and produced well above the ground. It is usually sheathed below by leaf bases, and in many species the third leaf is specialized as a sheath which envelopes the lower part of the stem. The upper half of the stem may be naked, or bear a specialized bract leaf (see above). The stem is densely (or occasionally sparsely) ciliate in all the species of section *Planifolia*, in several of section *Ciliata*, and in *G. ciliatula* and *G. scopulosa* (section *Monticola*) (all subgenus *Geissorhiza*) and in two isolated species, *G. intermedia* and *G. unifolia*, of subgenus *Weihea*, section *Angustifolia*.

Branching is variable, but certain species typically do not produce any branches, while extensive branching is characteristic only of several species of section *Monticola*, such as *G. ramosa*, *G. burchellii*, and *G. tabularis*. Branching is suppressed in all species of sections *Angustifolia* and *Ixiopsis*.

INFLORESCENCE

The inflorescence in *Geissorhiza* is, with a few exceptions, a spike of several flowers and may be more or less straight to flexuose. The number of blooms is variable depending on age and health of the plants and seasonal and soil conditions. A few scattered species in subgenus *Weihea* have solitary flowered stems, thus technically not true spikes. These include all three species of section *Tortuosa* (*G. corrugata*, *G. karooica*, and *G. spiralis*) and *G. delicatula* and *G. fourcadei* (section *Weihea*).

The spike is typically drooping in bud, and straightens gradually from the base as the flowers open progressively. This drooping is seldom evident in dried material and although not determined for all the species, appears to be a feature of the genus.

The flowers are subtended by paired, opposed bracts, a larger outer enclosing the smaller inner. The inner bract (sometimes called a bracteole), used very little as a taxonomic character, is a double structure with two main veins and a forked apex. While the inner bract may be as long or slightly longer than the outer bract, it is always smaller and narrower. Only in section *Engysiphon* are the inner bracts substantially shorter than the outer, and this is one of the diagnostic features of the section.

The outer bracts are usually herbaceous with a hyaline upper margin, and firm in texture, but often become dry from the apex soon after blooming. In subgenus *Geissorhiza*, sections *Planifolia* and *Ciliata*, the bracts become dry and ferrugineous in the upper half. This is particularly well developed in *G. aspera*, *G. monanthos*, *G. inflexa*, and *G. subrigida*. There is little to distinguish the bracts of other species with the exception of the members of section *Engysiphon* in which they are very large, up to 50 or 60 mm in some species, but only 15–20 mm long in *G. brevituba*, and much longer than the quite membranous inner bracts. *Geissorhiza humilis* and *G. hispidula* are distinctive in having sticky bracts, to which sand adheres even when the plants are dried.

FLOWER

Most species of *Geissorhiza* have a simple, actinomorphic flower with a short, straight, cylindric perianth tube and horizontally extended te-

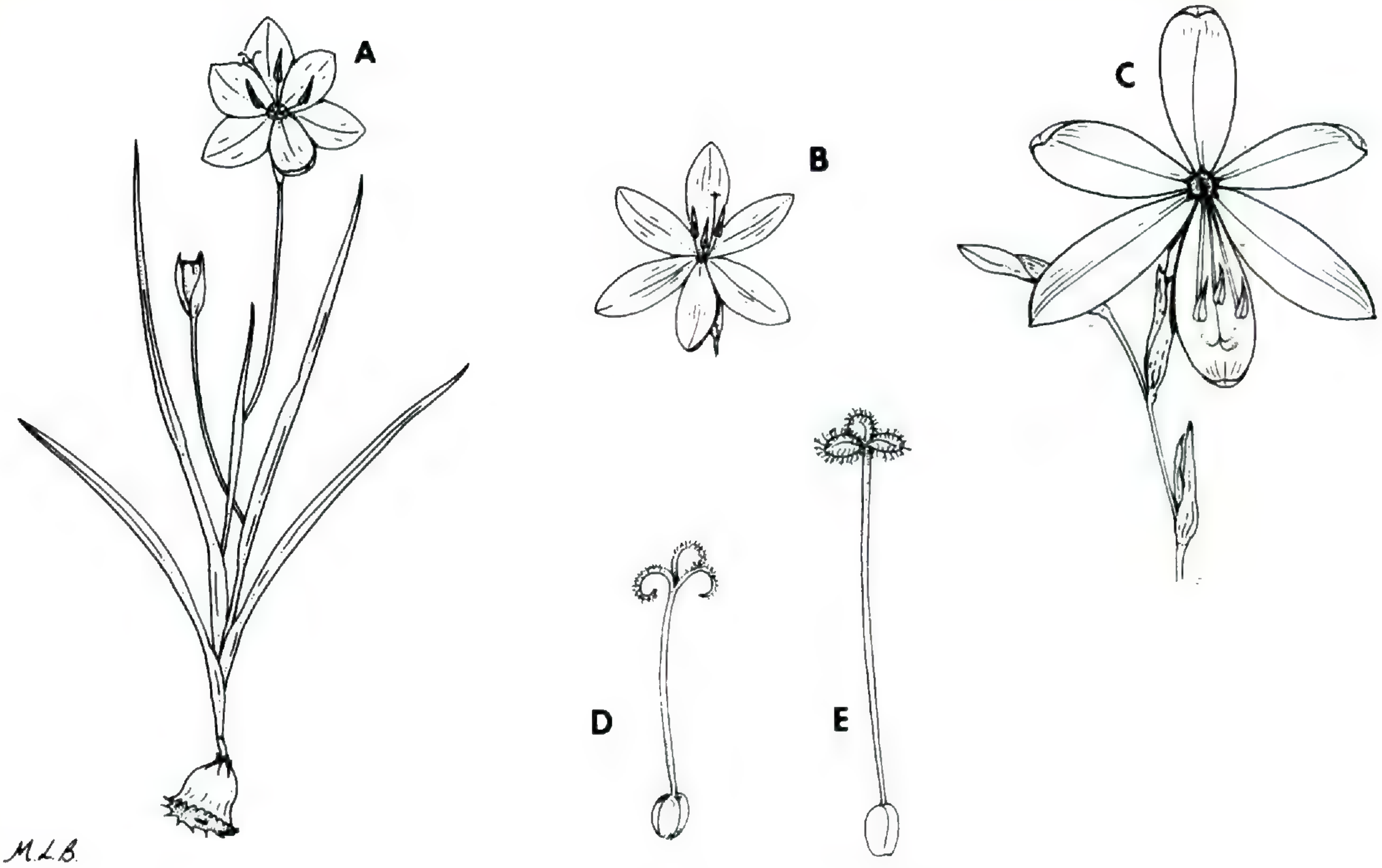


FIGURE 15. Floral features of *Geissorhiza*.—A. *G. ornithogaloides*, actinomorphic stellate flower with deflexed style.—B. *G. aspera*, stellate flower with unequal stamens.—C. *G. grandiflora*, zygomorphic flower with declinate stamens and style.—D. *G. imbricata*, typical style with short recurved branches.—E. *G. eurystigma*, the broad flat ciliate style branches found in this species (A–C life size; D–E ×2).

pals (Fig. 15A, B). The tube generally reaches to about the apex of the bracts surrounding the tube, but after fertilization it may become exserted a few millimeters due to the enlargement of the ovary. The style is slender and exserted well beyond the mouth of the tube and ultimately divides into three relatively short, recurved branches. The three stamens are usually symmetrically disposed, with the filaments inserted below the mouth of the perianth tube and well-exserted from the tube. The stamens vary considerably and are dealt with in more detail below.

Longer perianth tubes that are exserted for more than 1 or 2 mm from the bracts are unusual and are scattered throughout the genus. In subgenus *Weihea*, *G. ovata* (section *Weihea*), *G. nubigena* (section *Ixiopsis*), *G. stenosiphon* (section *Angustifolia*), and both *G. esterhuyseniae* and *G. cedarmontana* (section *Includanthera*) have unusually long perianth tubes. In section *Engysiphon*, the long perianth tube is accompanied by long bracts, and the tube may reach only to the apex of the bracts (*G. schinzii, G. bonae-spei*) or be exserted for some distance (*G. exscapa, G. confusa, G. tenella*).

Short perianth tubes that reach only to about the midline of the bracts are regarded as derived since they occur only in specialized species or sections, while moderately long tubes are found in the less specialized species and in related genera. These short tubes are characteristic of a few species in subgenus *Weihea*, notably *G. alticola* (section *Ixiopsis*), in sections *Planifolia* and *Ciliata*, and in several species of section *Geissorhiza*, all subgenus *Geissorhiza*. In these species, the bracts become dry at flowering time and are folded back in the midline by the outspread tepals.

Zygomorphic flowers appear to have evolved repeatedly in both subgenera (Figs. 5, 6, 11, 12, 15). In the zygomorphic flowers in *Geissorhiza*, the stamens are unilateral and decumbent, and lie above the anterior tepal (Fig. 15C). The style is also decumbent, and it lies under the stamens. This situation is unusual in Iridaceae where zygomorphic flowers typically have erect and unilateral stamens, arcuate under an erect and often hooded anterior tepal. In subgenus *Weihea*, zygomorphy is developed in *G. roseoalba* and *G. outeniquensis* (section *Weihea*), in *G. karooica* (section *Tortuosa*), and in all species of section *Engysiphon*, while in subgenus *Geissorhiza*, zy-

gomorphic flowers are found in *G. tulbaghensis* and *G. monanthos* (section *Planifolia*), in *G. radians* and *G. barkerae* (section *Geissorhiza*), and in *G. grandiflora* (section *Monticola*).

Flower colors of white to cream or shades of violet to purple are most common in *Geissorhiza* (Figs. 1–12), but all colors except shades of orange occur. Except for occasional mutants, populations and even species are uniform in their flower color. *Geissorhiza inflexa* stands out in having populations of white, purple, pink, or deep red flowers. Unusual color combinations occur in several species. In *G. barkerae,* most forms of *G. purpureolutea* and some of *G. brehmii* and *G. imbricata* (all section *Geissorhiza*), and in some populations of *G. inflexa* the cream to yellow flowers have a dark purple to brown center. *Geissorhiza eurystigma, G. radians,* and *G. mathewsii* (section *Geissorhiza*) and forms of *G. monanthos* have dark violet flowers marked with contrasting concentric bands of white and dark red (Figs. 10–11).

STAMENS

The three stamens typically have well-developed and equal filaments inserted in the perianth tube shortly below the mouth. The two species of section *Includanthera, G. cedarmontana* and *G. esterhuyseniae,* are remarkable in having very short filaments inserted near the base of the perianth tube, so that the stamens are entirely included in the tube.

An unusual feature of subgenus *Geissorhiza* is the presence in many species, of unequal filaments, one being consistently shorter, by at least 0.5 but up to 3 mm, than the other two (Fig. 15B). While this development appears to have arisen independently in each section (excepting section *Intermedia* where the character is not present), it is probably fundamental in the subgenus, although only expressed in certain species. In section *Monticola,* unequal filaments occur in all species except the very dwarf *G. ciliatula,* while in section *Planifolia,* unequal filaments occur consistently only in *G. inaequalis* and occasionally in *G. aspera* and *G. monanthos.* In section *Geissorhiza,* only *G. barkerae* and in section *Ciliata, G. heterostyla* consistently have a shorter filament, while this occurs occasionally in *G. louisabolusiae* (section *Geissorhiza*) and *G. leipoldtii* (section *Ciliata*).

The anthers are usually somewhat longer than the filaments, and erect to ascending. In those species with declinate stamens, the anthers are erect and thus held at right angles to the decumbent filaments. In *G. esterhuyseniae* and *G. cedarmontana* (section *Includanthera*), the anthers are included in the perianth tube. Anther size is a generally useful taxonomic character as it is fairly constant in a species, easy to measure, and a good indication of overall flower size.

GYNOECIUM

Style. The style is filiform, slender, and well exserted from the perianth tube. Ultimately it divides into three comparatively short and slender recurved branches (Fig. 15A–D). This character distinguishes the genus from the allied *Hesperantha* and varies very little. In *Geissorhiza cedarmontana* and *G. esterhuyseniae* (section *Includanthera*), however, the style is short and entirely included in the perianth tube while in the striking *G. stenosiphon,* the style may divide anywhere between the mouth of the perianth tube and the base of the anthers. The style typically diverges to some degree from an upright position in all species, but is decumbent and placed under the declinate stamens in zygomorphic species (Fig. 15C). In some populations of *G. heterostyla,* individuals may have either long (i.e., normal styles), medium, or short styles that reach only to the apex of the perianth tube (Bolus, 1930), hence the name given the species by Bolus. The anthers do not vary at all in length, so that the condition is not true heterostyly. This is presumably an adaptation to promote outcrossing.

Two species, *Geissorhiza eurystigma* and *G. mathewsii* (section *Geissorhiza*), have distinctive, broad flat style branches (Fig. 15E), described by Lewis (1954) as flat, thick, and crennate edged. The style branches of these two species are so unusual that they can immediately be recognized from this character alone.

Ovary. The oblong to ovoid ovary has little taxonomic value, and, apart from minor size differences, there is little to distinguish species on this character.

FRUIT

The fruit is a thin walled loculicidal capsule, typically more or less ovoid-oblong in shape. The ovary develops rapidly after fertilization, and generally grows to reach the apex of the bracts before maturing. The bracts enclose, to some extent, the young fruits but in the later stages of development the bracts become dry and broken.

The species of section *Engysiphon* stand out in having exceptionally long capsules that are more or less fusiform in shape. The capsules are entirely included in the long bracts of these species.

Seeds are basically turbinate to globose in shape with a persistent funicle and a testa of uncontorted epidermal cells with smooth surfaces. Deviations from this basic type include increasing compression, resulting in a more or less angular to irregular shape and the wrinkling and crumpling of the epidermal cells (Wagner & Goldblatt, 1984). Although the seeds of only a few species have been examined, seed structure appears relatively uniform and of limited taxonomic value, differences being mainly of size.

Cytology

Geissorhiza is relatively uniform cytologically. Basic chromosome number is $x = 13$ (Gwynne, 1958; Goldblatt, 1971), this coming from counts for 11 species. Additional studies here, including original counts for 32 species (Table 2), of which 30 are first reports for species, confirm the base number established in 1971. The cytological technique employed involved root tip squashes in contrast to the paraffin section method which I used in earlier studies of the genus. Details of the technique are described elsewhere (Goldblatt, 1979b, 1980) and consist of a pretreatment in hydroxyquinoline, fixation in absolute ethanol:glacial acetic acid (3:1), and a 5–6 minute hydrolysis in 10% HCl prior to squashing in orcein based stains.

A total of 41 species, over half the genus, is now known cytologically. Counts for most species, including as many as five or six populations of some, are diploid, $2n = 26$. Exceptions are *G. bracteata* (one count) and *G. inaequalis* (two counts), both tetraploid; *G. aspera* which has both diploid and tetraploid populations; and *G. bolusii,* where the five populations examined are triploid, $2n = 39$. B chromosomes have been recorded in *G. heterostyla,* $2n = 26$ and $2n = 26 + 2B$, *G. inflexa, G. bryicola,* and *G. tulbaghensis,* $2n = 26 + 1B$.

The basic number of $x = 13$ is somewhat unusual in Iridaceae, but it is shared by the closely related *Hesperantha* (Goldblatt, 1971, 1984) and the mono- or di-typic *Schizostylis* (Goldblatt, 1971). The karyotype is similar in all three genera and consists of fairly small meta- to submetacentric chromosomes that with the methods employed, range in size from 2.5–4 μm.

Infrageneric Classification and Cladistics

The classification adopted here rests on the primary assumption that the peculiar imbricate corm tunics found in many species of *Geissorhiza* arose once in the evolution of the genus. The recognition of the two subgenera proposed here is thus based on the nature of the corm tunics, species of subgenus *Geissorhiza* having imbricate tunics and species of subgenus *Weihea,* the presumably ancestral concentric tunics. Several other characters are correlated with the presence of imbricate corm tunics, all apparently specialized and restricted, or nearly so, to subgenus *Geissorhiza,* though not found in all species. These include leaf margin and midrib pubescence, corrugate leaves, ferrugineous bracts, unequal stamens, and stem puberulence (or ciliation).

Other major morphological specializations in *Geissorhiza* such as leaf margin and midrib thickening and development of floral zygomorphy seem to have arisen independently, in both the basal subgenus *Weihea* and the derived subgenus *Geissorhiza.* Both these types of specialization occur in other genera of Iridaceae and in this light seem secondary to the evolution of imbricate tunics, and in fact, both appear to have evolved more than twice in each subgenus.

Sectional Classification in Subgenus *Weihea*

Seven sections are here recognized in subgenus *Weihea,* sections *Weihea, Tortuosa, Pusilla, Includanthera, Angustifolia, Ixiopsis,* and *Engysiphon.* Subgenus *Weihea,* the largest with 18 species, corresponds closely to Foster's subsection *Foliosae.* It is diverse and includes several lineages, rather poorly differentiated, and is united by the unspecialized combination of concentric corm tunics and plane, usually ensiform to linear leaves without well-developed thickening of the margins or midrib. The flowers of the majority of species are also unspecialized, with tubes of moderate length, exserted and equal stamens. *Geissorhiza ovata* stands out in the section in having an unusually long perianth tube and nearly prostate, ovate leaves, while *G. roseoalba* and *G. outeniquensis* have unusually large flowers that are zygomorphic and declinate. *Geissorhiza fourcadei* stands out here in its terete leaves and large flowers that are solitary on the branches.

TABLE 2. Chromosome numbers in *Geissorhiza*. Original counts are marked with an asterisk (*). Previous counts were reported by Goldblatt (1971) except as indicated in the table, by Gwynne (1958).

Species	Diploid Number	Collection Data
G. arenicola	26*	W of Nieuwoudtville, *Goldblatt 7056* (MO)
G. aspera	26	without locality or voucher (Gwynn, 1958—as *G. secunda*)
	26*	Rondebosch Common, *Goldblatt 5350* (MO); Burghers Pos, Darling, *Goldblatt s.n.* (no voucher); Olifants River Valley, near Rondegat, *Goldblatt 5647* (MO)
	52	Cape Peninsula, Signal Hill, *Goldblatt 213* (BOL); Simonstown, *Goldblatt 520* (BOL)
	52*	Caledon, Albertyn road near Leeu River, *Goldblatt 4839A* (MO); St. James, Cape Peninsula, slopes below Boyes Drive, *Goldblatt s.n.* (no voucher)
G. barkerae	26*	N of Piketberg, *Goldblatt 6391* (MO)
G. bolusii	39	Bains Kloof, *Goldblatt 458* (BOL); Cape Peninsula, Grootkop, *Goldblatt 515* (BOL)
	39*	Villiersdorp, High Noon, *Goldblatt s.n.* (no voucher); Paarl, Simonsberg, *Esterhuysen 35281A* (MO); Jonaskop, Riviersonderend Mts., *Goldblatt 6444* (MO)
G. bonae-spei	26*	Cape Peninsula, opposite Cape Point Reserve, *Goldblatt 5267* (MO)
G. bracteata	ca. 52*	Hankey, Klein River Valley, *Goldblatt 4933* (MO)
G. brevituba	26	Piketberg, top of Versveld Pass, *Goldblatt 204* (BOL) (as *Engysiphon*)
G. bryicola	26*	Vogelgat, Hermanus, *Goldblatt 6741* (MO)
	26 + B*	Vogelgat, Hermanus, *Goldblatt 6742* (MO)
G. burchellii	26*	Swellendam, Langeberg, *Esterhuysen 35363* (MO)
G. cataractarum	26*	Caledon, cliffs above Bettys Bay, *Goldblatt 5355* (MO)
G. cedarmontana	26*	Cedarberg, Middelberg plateau, *Goldblatt 5145* (MO)
G. ciliatula	26*	Cedarberg, Middelberg, *Goldblatt 5144* (MO)
G. confusa	26	Bains Kloof, *Goldblatt 483* (BOL) (as *Engysiphon exscapus*)
G. corrugata	26*	Calvinia, *Goldblatt 3895* (MO)
G. erubescens	26*	Pakhuis Pass, *Goldblatt 6396* (MO)
G. exscapa	26*	top of Vanrhyns Pass, *Goldblatt 7061* (MO)
G. grandiflora	26*	Limietberg, Bains Kloof, *Goldblatt 6828* (MO)
G. heterostyla	26	Voelvlei, Sutherland, *Hall s.n.* (NBG); Calvinia, *Goldblatt 135* (J) (as *G. leipoldtii*)
	26*	Blomfontein road, W of Middelpos, *Goldblatt 5815* (MO); Grasberg road NW of Nieuwoudtville, *Goldblatt 6265* (MO)
	26 + 2B*	Humansdorp, E of town, *Goldblatt 5211* (MO)
G. cf. *hispidula*	26*	near Baardscheerdersbos, sandy flats, *Goldblatt 5377* (MO)
G. humilis	26*	Cape Point, near Reserve, *Goldblatt 5265* (MO)
G. imbricata subsp. *imbricata*	26	without locality, *Goldblatt 165* (J)
G. inaequalis	52	Vanrhyns Pass, *Goldblatt 129* (J); near Nieuwoudtville, *Goldblatt 275* (BOL)
G. inconspicua	26*	near George, *Vlok s.n.* (no voucher)
G. inflexa	26*	Caledon, Queen Anne-Eseljagt, *Goldblatt 2497* (MO); Caledon, W end of the town, *Goldblatt 6173* (MO)
	26 + 1B*	Tulbagh cemetery, *Goldblatt 5228* (MO)
G. juncea	26*	Cape Peninsula, Lions Head, *Goldblatt 4700* (MO)
G. kamiesmontana	26*	Kamiesberg, Rooiberg slopes, *Goldblatt 5770* (MO)
G. karooica	26*	Ghaap kop, Matjesfontein, *Goldblatt 6371* (MO)

TABLE 2. Continued.

G. longifolia	26	Pakhuis Pass, *Goldblatt 122* (J) (as *Engysiphon*)
	26*	N of Citrusdal, *Goldblatt 6267* (MO)
G. louisabolusiae	26	Citrusdal, *Goldblatt 247* (BOL)
G. malmesburiensis	26*	Malmesbury Commonage, *Goldblatt 6282* (MO)
G. nana	26*	near Swellendam, *Goldblatt s.n.* (no voucher)
G. ornithogaloides subsp. *ornithogaloides*	26	Caledon, *Goldblatt 214* (BOL) (as *G. nana*)
G. outeniquensis	26*	Outeniqua Pass, George, *Vlok 525* (MO)
G. ovata	26	Bot River, *Goldblatt 217* (BOL)
G. pusilla	26	Cape Peninsula, Signal Hill, *Goldblatt 196* (BOL)
G. roseoalba	26*	Paardevlei Mts., Attaquaskloof, *Vlok 706* (MO)
G. scillaris	26*	Elands Kloof, *Goldblatt 5245* (MO)
G. similis	26*	Bains Kloof, *Goldblatt s.n.* (no voucher); mts. above Clovelly, Cape Peninsula, *Goldblatt 7052* (MO)
G. splendidissima	26	Nieuwoudtville, *Goldblatt 347* (BOL)
G. tabularis	26*	above Skeleton Gorge, Table Mt., *Goldblatt 6726* (MO)
G. tenella	26*	S of Koeberg, *Goldblatt 7111* (MO)
G. tulbaghensis	26 + 1B*	Tulbagh cemetery, *Goldblatt 5227* (MO)

Section *Tortuosa* is a small segregate of section *Weihea,* restricted to the western Karoo. Two species have been added to the one assigned here by Foster. All three species are of small size, have large flowers, and are distinguished by having solitary flowered spikes.

The monotypic section *Pusilla* includes only the distinctive and taxonomically isolated Cape Peninsula species, *Geissorhiza pusilla.* It has a combination of features that suggest strongly a hybrid origin. Its concentric corm tunics are typical of subgenus *Weihea,* while the plane ensiform leaves are unusual for section *Weihea* in being pubescent. The very short-tubed flower and dry and ferrugineous floral bracts match exactly those found in sections *Geissorhiza* and *Ciliata.* This combination of the specialized features of subgenus *Geissorhiza* and the primitive concentric corm tunics of subgenus *Weihea* seems so discordant that an intersubgeneric hybrid origin is likely, although the possibility of an independent origin of the specialized short perianth tube and ferrugineous bracts cannot be discarded.

Section *Includanthera* comprises only *Geissorhiza cedarmontana* and the poorly known *G. esterhuyseniae,* corms of which have not been seen. The two species are united in having the stamens and the style included in the lower part of the long perianth tube. The affinity of these two species is uncertain but they are assumed to be a monophyletic offshoot of section *Weihea. Geissorhiza esterhuyseniae* has the plane ensiform leaves typical of section *Weihea* while the leaves of *G. cedarmontana* have strongly thickened margins and midribs. Section *Includanthera* is restricted to the higher mountains of the western Cape.

The specialized and derived sections *Angustifolia* and *Ixiopsis* are closely allied. Both have three or fewer, narrow leaves with heavily thickened margins and midribs and stems in which branching is suppressed. Section *Angustifolia,* corresponding largely to Foster's subsection *Filiformes,* comprises some 11 species, sharing unspecialized, usually small, actinomorphic flowers and small corms with hard woody tunics. Species usually have two basal leaves and a third, which is much smaller, inserted in the mid part of the stem, and partly sheathing. *Geissorhiza stenosiphon,* a very local endemic of the Cold Bokkeveld Mountains is remarkable in the section for its slender perianth tube some 4–5 cm long, and it stands out in the genus in having a style that divides between the mouth of the tube and the base of the anthers. This species, as well as *G. juncea* and *G. furva,* stands out in having terete, 4-grooved leaves. The poorly understood *G. intermedia* and *G. unifolia* are unique in sub-

genus *Weihea* in having lightly ciliate stems. The section is centered in the southwestern Cape, *G. unifolia* and *G. juncea* occurring as far north as the Cedarberg and *G. hispidula* ranging from the Cape Peninsula to the southern Cape near Albertinia.

The related section *Ixiopsis* comprises a close knit alliance of five species that are centered in the mountains of the southwestern Cape. Only one species, *Geissorhiza hesperanthoides* was known to Foster, who assigned it to his subgenus *Ixiopsis* together with three species subsequently removed to *Gladiolus*. All the species of the section occur in the southwestern Cape mountains between Bredasdorp and Tulbagh, and only *G. umbrosa* extends much outside this area, occurring as well on the Cape Peninsula and in the Cedarberg. In these species, the third leaf is typically reduced and entirely sheathing, and the corm tunics are soft in texture and either membranous or fibrous, most unusual for the genus.

Section *Engysiphon,* another close knit alliance, comprises seven species, united in having large, conspicuously veined zygomorphic and declinate flowers, usually with a very long perianth tube and long herbaceous bracts, the inner much smaller than the outer. The leaves have thickened to winged margins and the corms are typically large and have very hard woody tunics. The section, treated by Lewis (1941) as a separate genus and including one more species, here assigned to section *Weihea,* comprises two distinct assemblages, one in which the leaf has the thickened margins and midrib, also found in section *Angustifolia,* and the other in which the leaf has raised and winged margins that curve over the lightly thickened midrib. Despite the clear cut leaf differences, the two groups appear closely related and there seems no doubt that the section is monophyletic. The section has a markedly western distribution, species extending from the Caledon district north to Namaqualand.

SECTIONAL CLASSIFICATION IN SUBGENUS *GEISSORHIZA*

The species of subgenus *Geissorhiza* are united primarily by the possession of their characteristic imbricate corm tunics. These are remarkably uniform in the majority of species, especially in sections *Planifolia, Ciliata,* and *Geissorhiza,* being hard, dark in color, and regularly notched below. In section *Monticola,* there is a trend for the softening of the texture of the tunics, while in the two species of section *Intermedia* the corm tunics stand out as being pale in color. Section *Intermedia* is the only one in subgenus *Geissorhiza* in which none of the species have unequal stamens, a character that is probably a part of the genotype in the other sections although it is not always expressed. Thus it is, for basically negative reasons, that section *Intermedia* has been recognized, and it stands out as an isolated and residual group of the subgenus, the species united by their pale imbricate corm tunics and the frequent specialized feature of narrow leaves with strongly thickened margins and midribs.

Section *Monticola* comprises a range of species, in which branching is normally well-developed, the stamens are distinctly unequal and the corm tunics are often soft in texture with an accompanying tendency for the tunics to become displaced easily. It then often becomes difficult to be certain of the type of tunics in some species. However, well-preserved corms in a few specimens or the associated characters of the species is usually sufficient to determine the sectional position. Only two species of the section were known to Foster (1941) who assigned them to his otherwise monophyletic subsection *Filiformes.*

Section *Monticola* is centered in the mountains of the southwestern Cape, but it has a wide range, *G. ciliatula* occurring in the Cedarberg in the north and *G. burchellii* extending as far east as the Langeberg at Heidelberg.

Sections *Ciliata* and *Planifolia* appear closely allied, and were united by Foster in his subsection *Pubescentes* together with *G. pusilla.* They have in common, flowers with very short perianth tubes and bracts that become dry and ferrugineous above, during or after flowering. Some species of both sections have flowers with unequal stamens, and puberulous or ciliate stems, the latter found in all four species of section *Planifolia.* The only substantive difference between the sections is that the leaves of section *Planifolia* are flat, and usually smooth, while those of section *Ciliata* have the margins and midribs (and sometimes other veins also) raised and winged, and the edges of the wings ciliate. Two species of section *Planifolia* have zygomorphic and declinate flowers.

Section *Geissorhiza,* which corresponds with Foster's nomenclaturally illegitimate subsection *Ventricosae,* comprises a group of closely related species all having the leaves with strongly thickened margins and veins. In a few species, such

as *G. brehmii* and *G. louisabolusiae,* the leaves are very narrow or terete and 4-grooved, and in these the characteristic ribbing is developed on the typically inflated sheath of the uppermost leaf. Section *Geissorhiza* has radiated extensively in the flat plains of the western Cape, between Cape Town and Piketberg, but species extend as far north as the Nieuwoudtville Escarpment.

The formal taxonomic treatment, including descriptions and citation of types for the infrageneric classification outlined here, are presented in the systematic treatment.

CLADISTICS

A cladogram has been developed (Fig. 16) in which the subgenera and sections are grouped according to their shared derived characteristics (synapomorphies). The cladogram was constructed manually according to concepts established by Hennig (1966) and adapted by several botanists recently (Bremer, 1976; Humphries, 1981; Funk, 1982; to mention a few examples). As discussed in the preceding pages, the subgenera and sections are believed to be natural (monophyletic) assemblages. They can usually be distinguished on the basis of one or more specialized features, the polarity of which was determined by outgroup comparison and by generally accepted trends in the family.

The primitive section *Weihea,* as well as sections *Monticola* (subgenus *Geissorhiza*) and *Angustifolia* (subgenus *Weihea*), are undefined cladistically. Section *Weihea* is a residual grouping of presumably old and unspecialized species while sections *Angustifolia* and *Monticola* are defined phenetically. Section *Intermedia* (subgenus *Geissorhiza*) is a weakly defined group of two possibly residual species that may be misplaced in the subgenus. The major taxonomic characters are listed in Table 3 with their primitive (plesiomorphic) states assigned 0 and derived (apomorphic) states assigned 1 (or 2 or 3 if the character concerned has more than one derived state). The reasons for regarding the states as primitive or advanced are, unless obvious, discussed at length in the section dealing with the morphology of *Geissorhiza.*

It is perhaps unnecessary to point out that in making a cladogram of a group above the species level, only the presumed primitive state for the taxon concerned should be considered and not other states of the character that occur in that group. Thus section *Engysiphon* is the only one in which a zygomorphic flower can be used as a

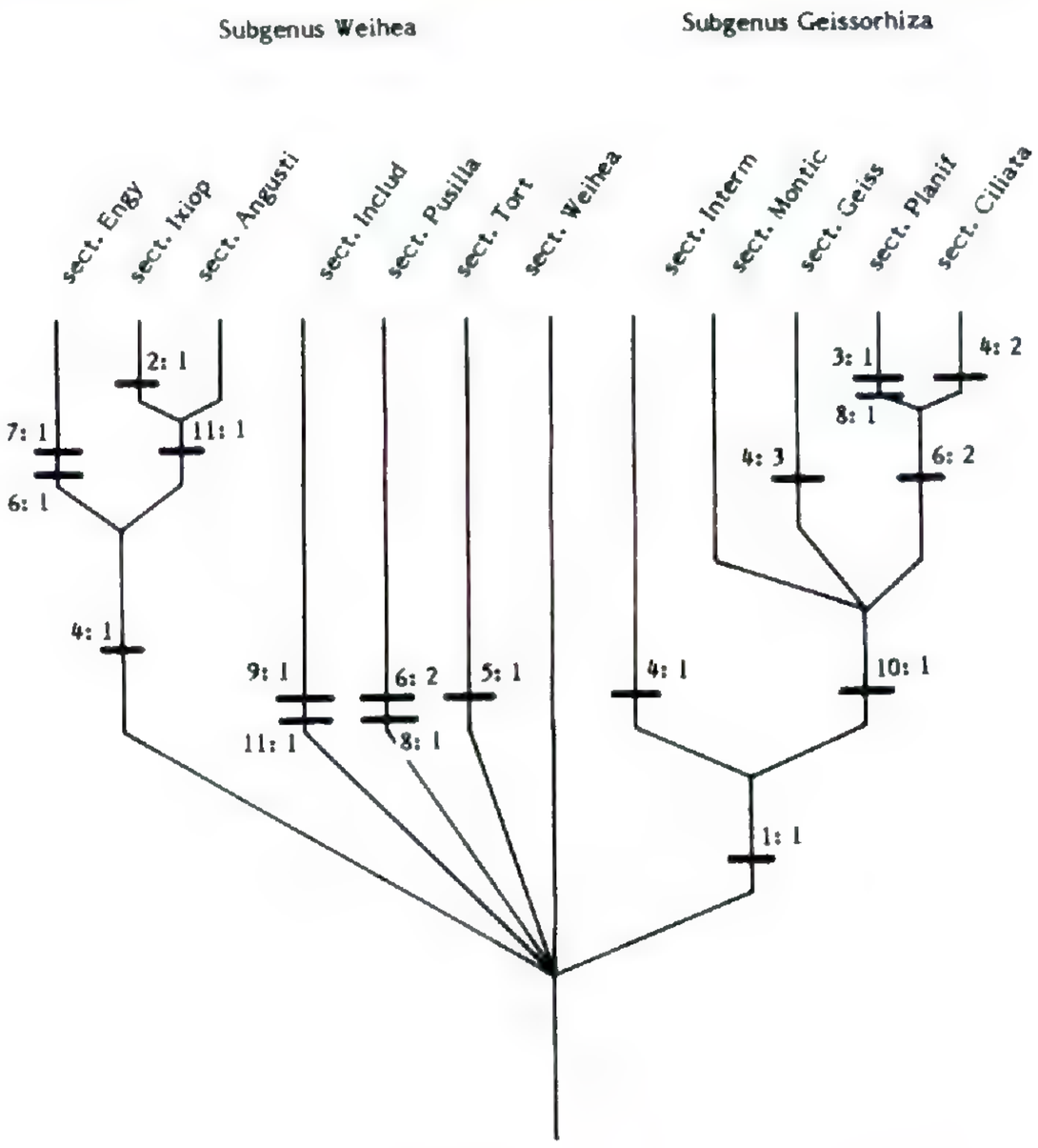


FIGURE 16. Cladogram of the sections of *Geissorhiza.* Section *Pusilla* is believed to be of hybrid origin between species of section *Weihea* and section *Ciliata.*

sectional character. In other sections, both zygomorphic and actinomorphic flowers occur but the basic state for each of these sections is presumed to be the actinomorphic flower.

One arbitrary assumption has been made in the case of the derived state for character 10, filaments unequal. This is, that whether the character occurs in all the species of the section or not, the derived state is regarded as a sectional character. I have done this because the character is an unusual one and it seems reasonable to regard it, in the absence of contradictory evidence, as part of the genotype of those sections in which it occurs although not always expressed. The alternative, to treat the character as newly evolved in each section in which it occurs, seems absurd since it would then be necessary to assume the independent origin of this very unusual character at least six times in subgenus *Geissorhiza* and nowhere else in Iridaceae.

My treatment of one main branch of the cladogram as a subgenus and several equivalent branches from the same node as sections of the second subgenus *Weihea* violates rigid cladistic theory. However, this seems justified in a situation where a basal and unspecialized group, section *Weihea* (species of which are probably little different from the basal stock of the genus) has given rise apparently independently to several lines, one of which has diverged and radiated to

TABLE 3. Important characters in *Geissorhiza* and their primitive and advanced states. The numbers 0 for primitive state, and 1, 2, or 3 for the derived state are used in the cladogram (Fig. 16) to indicate which characters have changed at branch points and their states.

Character Number	Primitive State 0	Advanced State 1, 2, or 3
1. Corm tunics	concentric	1. imbricate
2. Tunic texture	woody, brittle	1. membranous, soft/fibrous
3. Stem	smooth	1. puberulent to pubescent
4. Leaf blade	flat, ensiform	1. linear with thickened margins and midrib 2. linear with winged and ciliate margins and midrib 3. several ribbed and grooved
5. Inflorescence	spike of several flowers	1. solitary flowered
6. Bracts	green and herbaceous	1. very long and outer more or less two times the inner 2. ferrugineous above when plants dried
7. Flower	actinomorphic	1. zygomorphic and declinate
8. Perianth tube	as long as bracts	1. about half as along as bracts or 2. very long and well-exserted (unless the bracts also very long)
9. Stamens and style	well-exserted	1. included in lower part of the tube
10. Filaments	equal	1. one shorter than other two
11. Stem	branched	1. branching suppressed

such a degree that it is best to assign it higher rank than its sister groups rather than follow strict cladistic theory in classifying taxa. The possible intersubgeneric hybrid origin of section *Pusilla* discussed above is not reflected in the cladogram. Instead, section *Pusilla* is placed in subgenus *Weihea* (concentric corm tunics), and the features shared with sections *Geissorhiza* and *Ciliata* emerge as parallelisms.

I have not attempted to develop cladograms for the species in any infrageneric group as there seems little value in such effort in a large genus such as *Geissorhiza* in which there are few significant characters that define species and relationships appear reticulate in many sections due to convergence in many separate characters (homoplasy). In addition, some species that seem distinct on overall morphology appear to have no distinguishing features that can readily be polarized and used in a cladistic analysis.

GEOGRAPHY OF *GEISSORHIZA*

GENERAL TRENDS IN DISTRIBUTION

Geissorhiza is restricted to the southern African winter rainfall region (as defined by Goldblatt, 1976b, 1979a, 1981) which extends along the west coast from southern Namibia to the Cape Peninsula, and along the south coast to Port Elizabeth (Fig. 17). Only one species, *G. bracteata* occurs significantly outside this area. It ranges from the George district in the southern Cape into the southeastern Karoo and Eastern Cape, where some winter precipitation is usual but the area is usually regarded having a summer rainfall pattern. The genus is largely restricted to the Cape Floristic Province, which lies entirely within the winter rainfall region (Goldblatt, 1978). Only a handful of species occur outside the limits of the Cape Flora, two in the north in Namaqualand and four in the western and winter rainfall part of the Karoo, as well as *G. bracteata,* mentioned above.

The distribution patterns of the two subgenera, *Weihea* and *Geissorhiza,* differ in several ways. The more primitive subgenus *Weihea* is well represented in the southern Cape (Fig. 18), the eastern half of which receives substantial summer precipitation, and is often regarded as a region of year round rainfall. It is here that the majority of the least specialized species occur, most of which have comparatively wide ranges but there are amongst them several local endemics. Three species, comprising section *Tortuosa,* are unusual in this subgenus in being restricted to the western Karoo, where *Geissorhiza* is otherwise represented only by *G. heterostyla* (subgenus *Geissorhiza*). Subgenus *Weihea* has radiated ex-

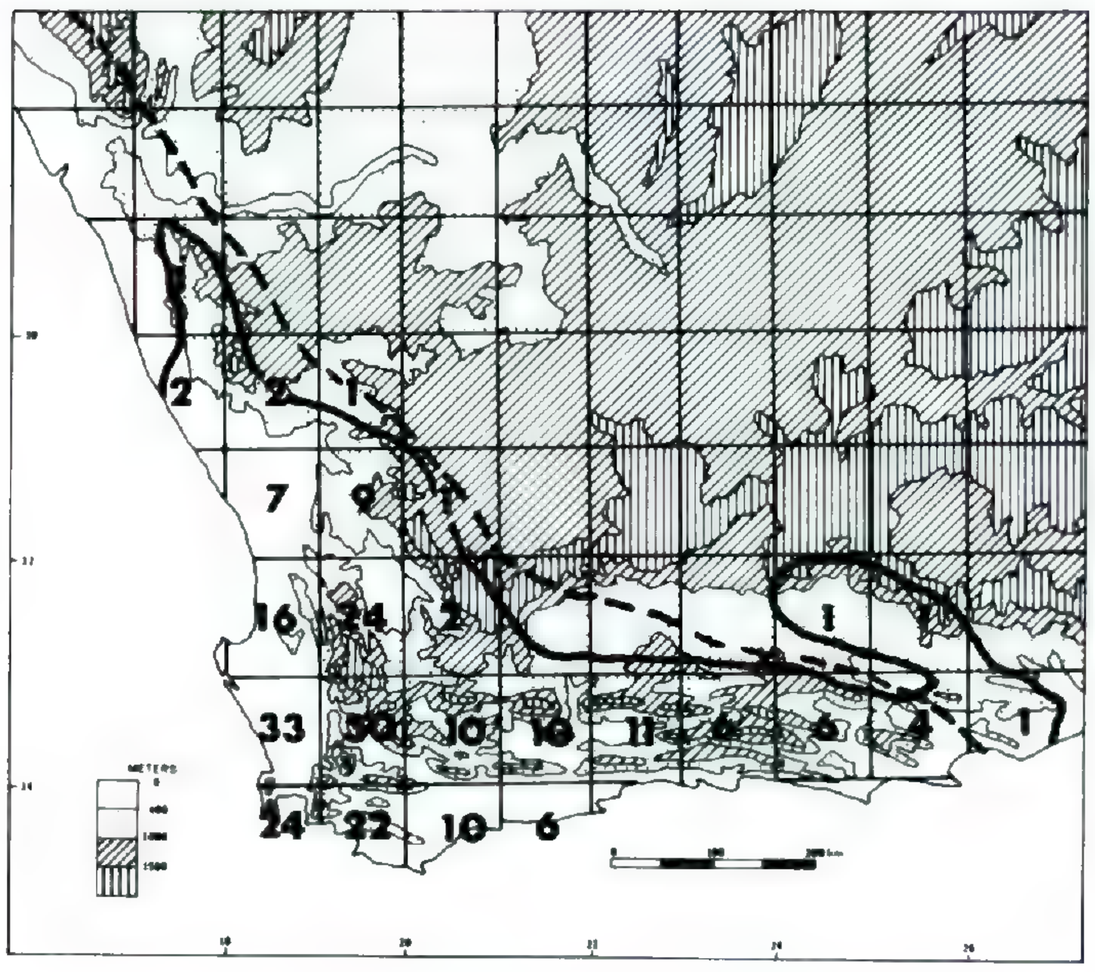


FIGURE 17. Concentration of species of *Geissorhiza* in southern Africa. Numbers indicate the total number of species recorded in each geographical degree square. The entire range of the genus is within the heavy line. The area usually regarded as receiving winter rainfall is to the west and south of the broken line.

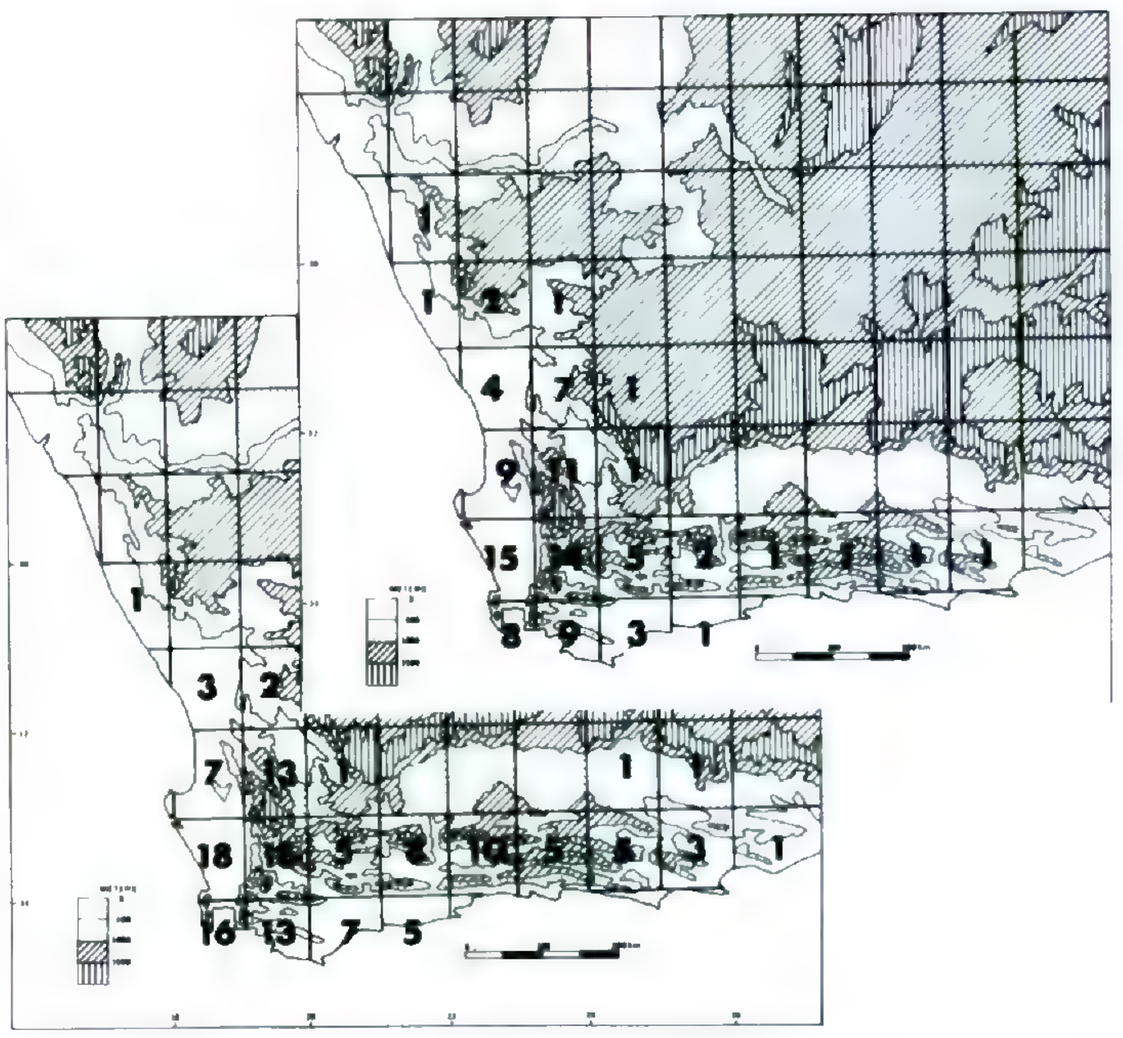


FIGURE 18. Concentration of species in the two subgenera of *Geissorhiza*: above subgenus *Geissorhiza*; below subgenus *Weihea*. Species are centered in the southwestern Cape, but substantial numbers also occur in the southern Cape especially in subgenus *Weihea*, whereas subgenus *Geissorhiza* has radiated extensively along the west coast, with species extending into northern Namaqualand.

tensively in the southwestern Cape, where two sections, *Angustifolia* and *Ixiopsis* have almost all their species. The relatively few species of subgenus *Weihea* that extend further north are amongst the most specialized in the alliance. These include the two species of the peculiar section *Includanthera*, and representatives of sections *Engysiphon* (*G. longifolia, G. confusa, G. exscapa*) and *Angustifolia* (*G. unifolia, G. juncea*).

Subgenus *Geissorhiza* is, in contrast, poorly represented in the southern Cape. It has its center in the southwestern Cape and is well represented northwards through the Cedarberg and Nieuwoudtville Plateau, while two species are endemic in Namaqualand. Despite the different overall distribution patterns in the two subgenera, both exhibit similar modes of extensive radiation in the southwestern Cape, both in the mountains and along the coastal belt from Cape Town to Piketberg. Subgenus *Geissorhiza* has radiated to a greater degree in the mountains of the northwest Cape and has two important centers of endemism here, one in the Cedarberg and one on the Nieuwoudtville Plateau and the Gifberg.

In all, 76 species of *Geissorhiza* occur in the Cape Floristic Region in a strict sense, and of these 73 occur exclusively here. Those occurring in the Cape Region as well as in the Karoo and Namaqualand are: *G. bracteata* (George in the southern Cape to Grahamstown and Cradock); *G. heterostyla* (southern Cape, the western Karoo, Nieuwoudtville escarpment and southern Namaqualand); and *G. exscapa* (Malmesbury to Hondeklipbaai in Namaqualand). *Geissorhiza namaquensis* and *G. kamiesmontana* are restricted to Namaqualand and *G. karooica, G. corrugata*, and *G. spiralis* are local endemics in the western Karoo.

The high concentration of species in the west (Fig. 17) suggests that the substantial radiation in *Geissorhiza* in this semi-arid, and summer dry area of rugged and varied landscape has been the result of strong selective pressure through extreme climatic variation during the glacial periods of the later Pleistocene (see chapter on Evolution). Contractions of ranges of species and the reduction and fragmentation of populations during periods of extremely unfavorable conditions presumably enhanced the tendency for divergence of species by the random effects of genetic drift in conjunction with locally differing selective forces. It is not surprising that concentration falls sharply in Namaqualand and in the interior where the climate is most arid. The relatively equable climate and higher, more evenly spread rainfall in the eastern southern Cape has evidently not provided the same stimulus to speciation that is so developed in the west, and this

TABLE 4. Centers of endemism in *Geissorhiza*.

SOUTHWEST CAPE CENTER	
Hottentots Holland-French Hoek Subcenter	*G. alticola, G. lithicola, G. nubigena*
Malmesbury Flats Subcenter	*G. darlingensis, G. eurystigma, G. furva, G. mathewsii, G. purpurascens, G. radians*
Cape Peninsula Subcenter	*G. bonae-spei, G. tabularis*
Bredasdorp Subcenter	*G. bryicola, G. schinzii*
Species occurring in more than one Subcenter of the Southwestern Center	*G. cataractarum, G. hesperanthoides, G. hispidula, G. humilis, G. pusilla, G. setacea, G. tenuis*
NORTHWEST CAPE CENTER	
Cedarberg Subcenter (here including the Piketberg)	*G. barkerae, G. brevituba, G. cedarmontana, G. ciliatula, G. erubescens, G. leipoldtii, G. louisabolusiae, G. minuta, G. stenosiphon, G. unifolia*
Great Winterhoek Subcenter	*G. esterhuyseniae, G. scopulosa*
Gifberg-Bokkeveld Mts. Subcenter	*G. arenicola, G. divaricata, G. inaequalis, G. splendidissima, G. subrigida, G. sulphurascens*
Species occurring in more than one Subcenter of the Northwestern Center	*G. longifolia*
LANGEBERG CENTER	*G. foliosa*
KAROO MT. CENTER	*G. nigromontana*
KNYSNA REGION	*G. elsiae, G. outeniquensis*
SOUTHEAST CAPE CENTER	none

area may be seen as a refugium for the primitive species of the genus.

CENTERS OF ENDEMISM

Geissorhiza is clearly a genus of the Cape Floristic Region and a predominantly montane one. It exhibits the patterns of endemism that have come to be seen as characteristic of the Cape Region (Weimarck, 1941) and the following discussion is framed in the context of Weimarck's phytogeographical subdivision of the Cape Floristic Region. Weimarck recognized six main centers of endemism and these are dealt with in sequence.

The Southwestern Center. The area of highest species concentration corresponds with Weimarck's Southwestern Cape Center where 46 species occur, 21 of these endemic. Remarkably large numbers of species occur on the coastal plain north of the Cape Peninsula (Weimarck's Malmesbury Flats Subcenter) and on the mountain complex that includes the Kogelberg, Hottentots Holland, French Hoek, Du Toits Kloof, and Bains Kloof Mountain Ranges (the French Hoek and Hottentots Holland Subcenters). Six species are restricted to the Malmesbury Flats (Table 4) and two to the Hottentots Holland-French Hoek Subcenters. The Cape Peninsula Subcenter is small but has two endemic montane to submontane species (Table 4). These presumably evolved as a result of their separation from the main populations of their relatives that grow inland across the inhospitable Cape Flats barrier that isolates this subcenter. The Bredasdorp Subcenter, so frequently an important center of radiation for taxa of the Cape Flora, has only two endemics (*G. schinzii, G. bryicola*), also both montane to submontane. Most of the mountain species of this subcenter also occur in the Hottentots Holland Subcenter, the mountain ranges being continuous or almost so. The lowland species are either shared with the Langeberg Center (*G. nana*) (there is virtually no barrier to migration between the lowlands of the two regions) or the Malmesbury Flats (*G. inflexa*) (isolated by substantial mountain barriers).

The Northwestern Center. This includes two important subcenters, the Great Winterhoek

Subcenter, and the Cedarberg Subcenter (Table 4), while Weimarck admits two noncontiguous areas, the Kamiesberg and Hantam-Roggeveld Subcenters as a part of the Northwestern Center. There are two species restricted to the Great Winterhoek Subcenter and ten to the Cedarberg Subcenter. This area includes several of the most specialized species in the genus including *G. stenosiphon,* the two species of section *Includanthera, G. esterhuyseniae* and *G. cedarmontana.* Evidently the fairly rich development of the Cape flora on Cape Sandstone soils north of the Cedarberg, on the Gifberg and Bokkeveld Mountain complex was unknown to Weimarck, and I feel compelled to extend the Northwestern Center to include this area, which I recognize as the Gifberg-Bokkeveld Subcenter. The significance of this subcenter is particularly evident in Iridaceae, not only in *Geissorhiza* but in several other genera, notably *Hesperantha, Gladiolus,* and *Sparaxis* as well as in other monocots. The *Geissorhiza* endemics in this subcenter include *G. subrigida, G. divaricata, G. arenicola,* and *G. splendidissima,* all closely allied species of section *Ciliata* and *G. sulphurascens,* section *Geissorhiza.*

Neither the Kamiesberg nor the Hantam-Roggeveld Subcenter is regarded today as part of the Cape Flora, but there is a development of vegetation that has several elements clearly of Cape origin. Two species of *Geissorhiza, G. tortilis* and *G. corrugata* are endemic in the Hantam-Roggeveld area while *G. heterostyla* is common but it extends through the interior southwestern Cape and the southern Cape to Port Elizabeth. On the Kamiesberg, there are only two species, the endemic *G. kamiesmontana* and *G. namaquensis,* that extend northward to Namaqualand to the southern Richtersveld. Neither species is common, and they seem to be restricted to areas of higher moisture availability in this arid country.

The Southern Cape Centers. Few species of *Geissorhiza* in the southern Cape fall conveniently into the four phytogeographic divisions recognized here by Weimarck (the Karoo Mountain, Langeberg, Knysna, and Eastern Centers). There is only one species, *G. nigromontana,* endemic to the Karoo Mountain Center, one to the Langeberg Center, *G. foliosa,* and two to the Knysna Region, *G. outeniquensis* and *G. elsiae.* No species is endemic to the Eastern Center and its separation from the Knysna Region has no significance for *Geissorhiza* or for Iridaceae in general. In the combined southern Cape Centers, the endemics include *G. fourcadei, G. roseoalba,* and *G. inconspicua,* in addition to the more restricted *G. foliosa, G. outeniquensis, G. nigromontana,* and *G. elsiae.* This is not surprising since the Langeberg and Outeniqua Mountains extend virtually continuously from Montagu in the west to Humansdorp in the east, and the few minor gaps seem not to have affected the distribution of *Geissorhiza* species to any degree. The drier interior southern Cape mountains that include the small and somewhat isolated Little Karoo ranges (Rooiberg, Warmwaterberg, Kammanassie Mountains) and the Swartberg Mountains have a poor *Geissorhiza* flora in contrast to the apparently climatically and geologically similar western Cape mountains. Reasons for this are not clear but presumably they had very different climatic histories.

In summary, the southwestern part of the Cape Floristic Region is the center for the evolution and radiation of *Geissorhiza.* Within the region are several important centers of endemism. The most important of these are the coastal plain between Cape Town and Piketberg (Weimarck's Malmesbury Flats Subcenter) and the southwestern Cape mountain complex between Cape Hangklip and Tulbagh (Weimarck's French Hoek and Hottentots Holland Subcenters). The mountains of the west coast, the Northwestern Center, constitute another important center for speciation especially for subgenus *Geissorhiza;* and a Gifberg-Bokkeveld Mountain Subcenter, not recognized by Weimarck, emerges as a major center of endemism in *Geissorhiza* as well as many other geophytic monocots.

Ecology

Species of *Geissorhiza* have radiated extensively in the southwestern Cape and have come to occupy a greater variety of niches than most other genera of Iridaceae, here or elsewhere. Perhaps the most important ecological distinction in the genus is an edaphic one. Species are generally found on either a shale-derived clay soil or a sandstone or granite-derived sandy soil. The importance of soil type in the distribution of Cape taxa (Goldblatt, 1978) has been discussed by several authors for various genera, notably Dahlgren (1968) for *Aspalathus* (Leguminosae) and Rourke (1972) for *Leucadendron* (Proteaceae) and it seems particularly significant in geophytic taxa (Goldblatt, 1976b, 1979a, 1981).

In *Geissorhiza,* which is almost entirely restricted to the area of the Cape Flora, relatively

few species grow on the heavy clay soils that are covered by renosterbosveld, a characteristic microphyllous scrub vegetation. This habitat is shared with numerous geophytic taxa of several families. These soils are found mainly on flats or lower mountain slopes. They are relatively well watered, especially along the coast, in the wet winter months, but dry out rapidly in the later spring when much of the geophyte flora of these areas blooms in a four to six week period in the spring. Common species of this habitat are *G. inflexa, G. leipoldtii,* the rare and rather local *G. tulbaghensis* (section *Planifolia*), *G. nana* and *G. bracteata* (section *Weihea*), and *G. ornithogaloides,* to mention some of the more significant examples. *Geissorhiza erubescens* (section *Ciliata*) and *G. longifolia* (section *Engysiphon*) are montane to submontane species, but they occur on the upper shale band of the Table Mountain Series. This is a broad layer of shale located in the upper part of an otherwise sandstone geological system, of which the Cape mountains are largely composed.

The very characteristic nutrient poor quartzitic sandy soils of the Cape region have a quite different range of *Geissorhiza* species, and it is on these soils that most of the radiation in the genus has occurred. The lowland alluvial sands have a very rich *Geissorhiza* flora. These soils also dry out fairly rapidly at the end of the wet months and flowering is condensed into an eight week period, but lasting longer than in the clay-loving species. Most common on flats and lower mountain slopes in sandy soil is *G. aspera,* of the southwestern and western Cape, while *G. heterostyla* is found in similar habitats in the southern Cape. Curiously, outside the Cape Region, *G. heterostyla* occurs on heavy clay soils in the Roggeveld, which seems a strange contradiction. Species of section *Angustifolia* are also well suited to lowland alluvial sands, and *G. humilis* and *G. hispidula* are common here in the western Cape, while the related, very local endemic *G. darlingensis* occurs near Darling in similar sites.

In seasonally moist sites in the southwestern Cape, section *Geissorhiza* has speciated to an unusual extent, and all the species of section *Geissorhiza* occur in such habitats. *Geissorhiza purpureolutea, G. imbricata,* and *G. barkerae* occur in moist sandy flats between Cape Town and Piketberg, while *G. brehmii* favors even wetter situations in this area and is semi-aquatic, growing in seasonal pools. In the Darling district where the parent rock is granite, *G. radians, G. mathewsii,* and *G. eurystigma,* also of section *Geissorhiza,* fill this seasonally wet lowland habitat. Further north this wet sandy habitat is occupied by *G. louisabolusiae* in the Olifants River Valley and by the closely allied *G. sulphurascens* on the Nieuwoudtville escarpment. Only a few species in other sections grow in this habitat, notably *G. setacea* (section *Weihea*) which occurs between Cape Town and Gouda.

The characteristically montane species all grow in well-drained, nutrient poor soil derived from rocks of the Cape Sandstone series. Although these soils are very low in nutrients and have poor water retaining properties, the mountains themselves receive a higher rainfall than the surrounding valleys and flats, and this appears to have allowed geophytic groups such as *Geissorhiza* to have filled some unusual niches. In montane marshy sites, *G. umbrosa* is often common in the early summer when the surrounding vegetation has been burned. Damp southerly facing slopes often harbor *G. hesperanthoides, G. nubigena,* and open rocky situations are a habitat for *G. ramosa, G. grandiflora,* and *G. burchellii.* The flowering season is later and longer in the higher mountains, presumably because of cooler temperatures and because moisture may be available for a longer time, or may even be permanent, as for the January flowering *G. cataractarum* and *G. outeniquensis,* both species of stream and waterfall edges.

Species of section *Engysiphon* often occur on dry mountain slopes and flower in the early summer. In the Caledon district, the section is represented by *G. schinzii, G. confusa* occurs in the mountains to the north while *G. brevituba* is restricted to the isolated Piketberg Mountains and *G. bonae-spei* to the southern Cape Peninsula.

POLLINATION

The pollination biology of *Geissorhiza* is largely unknown, but the genus is believed to be mainly bee pollinated (Vogel, 1954: 101, 115). Vogel suggested this on the basis of the predominant flower form in the genus: the flowers are radially symmetric, typically short-tubed, open during the day, and are brightly colored, often violet to purple. He cites only a few direct observations to support his hypothesis, including those of Elliot (1891), who made numerous records of insect visitors on southern African plants. Elliot found that *Geissorhiza aspera* (as *G. secunda*) was visited by several species of bees. His record of a dipteran visiting '*Ixia excisa* Thunb.' is also probably for *Geissorhiza, I. excisa* being an early synonym for the distinctive *G. ovata.* Vogel re-

cords the observations of Hans Herre of bee pollination for *G. radians* (as *G. rochensis*) and presumably his own for a few more species: *G. splendidissima, G. furva,* and a species identified as *G. ramosa,* all from 'Little Namaqualand,' probably the northwestern Cape.

Vogel suggests that the pale, small flowers of *G. juncea* are moth pollinated, on the assumption that they open in the evening. The species is, however, day blooming and very short-tubed therefore, moth pollination is unlikely. If direct observation was actually involved, then a misidentification must have been made. Vogel also suggests that the few long-tubed species of *Geissorhiza* may be butterfly pollinated, mentioning by name *G. fourcadei.* On the basis of their flower form, he predicts that *G. ovata* and '*G. namaquensis,*' perhaps *G. kamiesmontana,* also have this type of pollination. Elliot's observation of a dipteran visiting *G. ovata* would seem to contradict butterfly pollination for this species.

Clearly more data is required before the somewhat confusing and uncritical suggestions made by Vogel can be accepted. It seems likely that pollination studies in *Geissorhiza* will be of considerable value in understanding the evolution and speciation in this large genus in which flower form is often the major or only distinction between related species.

CONSERVATION

There are a large number of very localized species in *Geissorhiza* and by certain definitions all of these may be regarded as potentially endangered. However, all of those that occur in mountain habitats appear reasonably secure because this habitat is not likely to be modified to any appreciable degree in the foreseeable future except by too frequent fires and the spread of alien woody vegetation that poses a severe threat to some of the Cape mountain vegetation (Goldblatt, 1978; Stirton, 1978). As far as I am aware, there are at this time no mountain species of *Geissorhiza* that are in any way endangered. The current practices of conservation and management conducted by the South African Department of Forestry, which controls a large part of the Cape mountains, is in fact likely to improve the conservation status of what remains of this vegetation.

The situation is, however, very different in the lowlands, particularly on the coastal plain north of Cape Town as far as Piketberg. Here the spread of agriculture and the growing population are placing considerable pressure on what little remains of the rich and highly endemic flora of the area. This coastal plain is one of the two major centers of radiation of *Geissorhiza* and of the approximately 35 species that occur here, 15 have the larger part of their range in this relatively small area, and six species, *G. purpurascens, G. darlingensis, G. eurystigma, G. mathewsii, G. furva,* and *G. radians* are endemic. A further two at least, *G. setacea* and *G. purpureolutea,* are nearly restricted to this area and are similarly threatened. Of the species mentioned above by name, only *G. radians* (better known as *G. rochensis*) has a wide distribution throughout the coastal plain. Although now reduced to fewer and smaller populations, it is still relatively common. The exact status of the other species mentioned is uncertain but all must be regarded as severely threatened in some degree. *Geissorhiza darlingensis* and *G. mathewsii,* are both restricted to few sights and require protection. Both occur in the Darling area, northwest of Cape Town in a rich agricultural region, and the changes in agricultural practice in recent years including aerial spraying of weed killers and insecticides, as well as the enrichment of the soil through annual application of fertilizers, have changed the habitat of what is left of the native flora so that it seems probable that some of the rarer coastal plain endemics may become extinct within the next few decades through habitat loss or impoverishment. As demonstrated by Parker (1982), there is very little undisturbed habitat along the west coast and the need for preserves to save what remains of this once rich and interesting flora should be given the highest priority.

To the north, the situation is similar in lowland areas and *Geissorhiza louisabolusiae,* endemic to the mid Olifants River Valley and adjacent valleys, is near extinction as a result of the spread of agriculture in this area and the draining of the semi-marshy situations to which it is restricted. The several local endemics of the Nieuwoudtville escarpment have always been very local in range and should be considered under pressure. Flat sandy areas here are increasingly being put to agricultural use and the striking *G. splendidissima,* to name one species, is becoming particularly rare and should be regarded as seriously endangered.

EVOLUTION

It seems likely that the ancestral stock that gave rise to *Geissorhiza* and the closely allied *Hesperantha* differentiated in upland eastern

southern Africa in the Miocene (26–5 Ma) when the climate of this area was becoming increasingly seasonal and the predominant forest vegetation was giving place to larger areas of open grassland and heathland (Axelrod & Raven, 1978; Goldblatt, 1983). A seasonal climate presumably provided the selective force for the deciduous and geophytic habit. During the Miocene, Africa moved rapidly some 10° northwards and at this time the southern and western Cape must have been well forested perhaps with local areas of drier climate suitable for geophytes.

Conditions along the wetter parts of the southern Cape coast today are probably similar with forest clothing the valleys and the southern mountain slopes but locally either rock outcrops, shallow soils or rainshadow effects provide suitable habitats for species of *Geissorhiza* and many other geophytic taxa. It was not until the late Pliocene or the Pleistocene, however, that a Mediterranean, winter wet and summer dry, climate developed along the Cape southwestern and west coasts and truly arid conditions prevailed to the interior and further north along the west coast. Thus the large numbers of species of *Geissorhiza* that occur today in the southwestern Cape and seem so specialized in comparison to most of the species of the southern Cape, probably did not exist until relatively recent times. Many probably evolved only during the Pleistocene as the distinctive Cape climate became established. The climatic fluctuations of the Pleistocene, reasonably well documented along the Cape west coast at Rietvlei and Langebaan, are believed to have provided the stimulus for the burst of radiation that produced the wide array of species of *Geissorhiza* in the southwestern Cape.

The unspecialized southern Cape species such as *Geissorhiza inconspicua, G. bracteata,* and *G. foliosa* have probably diverged very little from their ancestors that were present in the late Miocene and the Pliocene. They probably evolved slowly by a process of phyletic evolution (G. G. Simpson, 1953; B. B. Simpson, 1973) rather than true speciation. These species or their ancestors probably migrated from the forests of southeastern Africa into the eastern and southern Cape when habitats opened up for them as aridity spread southward in the Pliocene and Pleistocene and the southern forests began to shrink.

The establishment of a Mediterranean climate in the extreme southwestern Cape during the Pleistocene and the recorded climatic fluctuations of the time are known to have led to major shifts in the vegetation belts here, with the forest alternately contracting to sheltered sites and then expanding into the lowlands where they do not occur today. These shifts must have affected the ranges and population sizes of species of *Geissorhiza* very strongly, with the resulting local extinctions and fragmentation of populations that are believed to precede geographic speciation. Increasing aridity also accentuated habitat differences and increased the diversity of ecological niches available to species.

The large numbers of species that occur along the west coast and in the adjacent mountains are thus seen as having evolved under circumstances of increasing but fluctuating aridity, more or less in place in a relatively short time, following the classical model for geographic and ecological speciation or a combination of these. The main trends of phenotypic specialization are xeromorphic. They include a reduction in the number of leaves, decrease in leaf surface area, the development of heavy marginal and costal thickenings alternating with grooves, and leaf edge ciliation. Stem modifications include the development of pubescence, the reduction of branching and of flower number in the spike. Similarly, floral modifications such as the decrease or increase in the tube length are associated with specialization for different pollinators, a feature not evident among the primitive, less drought adapted species. Such floral specializations seem consistent with adaptation to drier climates, where bees and other insects with specialized pollination behavior are more numerous.

Subsequent migration and the spread of newly evolved forms must certainly have occurred but time and physical barriers have limited their spread throughout suitable areas of the southwestern Cape, and these factors have combined to produce the patterns of distribution that prevail today. The centers of endemism and geography of the genus are discussed more fully in the section on Geography.

Section *Includanthera* affords a striking example of quantum evolution or speciation (G. G. Simpson, 1953; Grant, 1977), usually regarded as distinct from geographic speciation. In quantum speciation, novel phenotypes appear to have been produced abruptly, without a series of intermediates among their allies. The two species of section *Includanthera* are remarkable in their long-tubed flower with the stamens in-

cluded in the middle part of the tube and the style and style branches more or less rudimentary and no more than a few millimeters long. The species with this remarkable flower might seem better treated as a separate genus but examples of similar specialization occur in a few isolated species of *Hesperantha* (Goldblatt, 1984) and in some forms of *Ixia paniculata* (Lewis, 1962). The examples of convergence for included stamens and styles makes it seem best to maintain species with this character combination in the genera to which they are allied.

Speciation through gross chromosome mutation is apparently rare in *Geissorhiza*. Examples of polyploid speciation include *G. inaequalis* and possibly *G. bracteata*, both tetraploid, but the single count for the latter is not sufficient for this hypothesis to be accepted without reservation. In *G. aspera* where tetraploid populations were initially found, further examination has revealed the presence of diploid populations as well, and the possibility of its polyploid origin is no longer tenable. *Geissorhiza bolusii*, however, seems to have arisen through allopolyploid hybridization. The five populations counted are all triploid, $2n = 39$. The ancestors of this widespread, sexually sterile species have not been identified, but the morphologically similar and sexually fertile *G. ovalifolia* (chromosome number unknown) is very likely one of the progenitors of *G. bolusii*.

With about half the species of *Geissorhiza* known cytologically, it is not possible to fully assess the role of chromosomal mutation in speciation, but it seems likely to have been small as in most other genera of Ixioideae in Africa (Goldblatt, 1971), with the notable exception of *Romulea* (De Vos, 1972).

Taxonomic History

The first species of *Geissorhiza* known to science were described during the later eighteenth century, and assigned to the broadly circumscribed genus *Ixia*. When *Geissorhiza* was first regarded as distinct from *Ixia* (Ker, 1803, 1804) some 15 different species had been described, three by de la Roche (1766), one each by Bergius (1767), Burman f. (1768), and Linnaeus f. (1782), eight by Thunberg (1783, 1800, 1803) and two by Ker. Ker actually admitted only 11 species to *Geissorhiza* (one of which is *Romulea* sp. and another a nomen nudum but it is probably the species currently known as *G. furva* Ker ex Baker). He was apparently unaware of Burman's *G. ovata*, of which *G. excisa* (L. f.) Ker is a synonym, and of three Thunberg species, *G. exscapus* published in 1800 (as *Gladiolus*) and *G. monanthos* and *G. radians* published in early 1803.

Of these early botanists, the contribution made by Thunberg is by far the most important (Goldblatt, 1983). Thunberg actually collected specimens of at least 13 species during the three years he spent exploring the Cape (1772–1775). He regarded these as belonging to eight different species, seven assigned to *Ixia* and one, *G. exscapus* to *Gladiolus*. Thunberg treated all but two, *I. secunda* sensu Berg. and *I. hirta* Thunb. (nom. superfl. pro *I. inflexa* de la Roche) as new. The identity and typification of the species described by Thunberg is complex and although the Iridaceae of Thunberg's Herbarium were examined and reviewed by Brown in 1928, several problems were only resolved after a recent reexamination of the collection (Goldblatt, 1983). The typification of the three species of *Ixia* described by Daniel de la Roche and now known to belong in *Geissorhiza* is also problematic (Goldblatt & Barnard, 1970). Authentic material was discovered in 1969 and as a result several de la Roche species could for the first time be identified and typified, including the long misinterpreted *G.* (*Ixia*) *inflexa*. No authentic material of *G.* (*Ixia*) *imbricata* was discovered and a neotype now identifies this species (Goldblatt & Barnard, 1970). The name of a third species, *I. secunda* (syn. *G. eurystigma*) cannot be transferred to *Geissorhiza* as the epithet is occupied in the genus.

The important cycle of collecting in the period 1820–1830, by Ecklon and Zeyher, by Drège, and to a lesser extent by Pappe, resulted in the discovery of many more new species of *Geissorhiza*, collected in large sets and widely distributed among European, North American, and South African herbaria. Ecklon (1827) enumerated his and Zeyher's collections, several of these being new species, but mostly as nomina nuda. Ecklon also introduced the new generic name *Weihea* (also without description) for the unusual *G. ovata* (as *W. excisa*) as well as *G. bracteata* (as *W. elatior*). *Weihea* was validated as a subgenus by Foster (1941) and is recognized here with a much broader circumscription. Amongst Ecklon's 18 listed species of *Geissorhiza* and *Weihea*, 13 are apparently new, but only two, *G. rosea* and *G. candida* can be regarded as legitimate. Most of the Drège, and Ecklon and Zeyher collections were

studied later in the nineteenth century by Klatt (1866, 1882) and by Baker (1876, 1892, 1896), both of whom described several new species from their collections.

Baker's treatments of Iridaceae in his "Handbook of the Irideae" (1892) and in "Flora Capensis" (1896), essentially identical, are a watershed for the taxonomy of the family in southern Africa. Baker recognized 29 species in *Geissorhiza* (six of which have since been transferred to *Hesperantha, Ixia,* and *Gladiolus*) and three more were assigned either to *Acidanthera* (*G. exscapa* as *A. tubulosa*; and *G. tenella* as *A. rosea*) or *Romulea* (*G. spiralis*). Klatt's (1895) treatment in the "Conspectus Florae Africae" is seldom given much attention by systematists, but it is noteworthy that he recognized 40 species in *Geissorhiza*. Of these some five belong to other genera, leaving the genus still appreciably larger than Baker treated it a year later.

Botantical activity in southern Africa accelerated in the late nineteenth century, when important collections of *Geissorhiza* were made by Peter MacOwan, Harry Bolus, Arnold Penther, and notably Rudolph Schlechter. Baker described three species based on Penther collections that he saw after the "Flora Capensis" had been published. Schlechter's collections were described partly by Schlechter himself (1899), but only one of his species, *G. hesperanthoides,* is currently recognized. Later, Foster (1941) described several new species based on the Schlechter collections, of which *G. burchellii, G. malmesburiensis,* and *G. leipoldtii* are currently recognized.

The modern cycle of collecting, initiated by H. M. L. (Louisa) Bolus in the 1920s continued essentially without a break until today. Louisa Bolus and her students, W. F. Barker and G. J. Lewis, as well as R. H. Compton made important collections of Iridaceae generally. Their activity resulted in the discovery of several new species of *Geissorhiza* (Bolus, 1930, 1931; Bolus & Lewis, 1933) and extended the known ranges of many more. Foster's studies, published at this time, however, benefited little from this work, and he saw only the few duplicates that then reached European herbaria. Nevertheless, Foster (1936, 1941) clarified the nomenclature of several previously problematic species, and he described as new some 11 species: *G. burchellii, G. louisa-bolusiae, G. sulphurascens, G. leipoldtii, G. ovalifolia, G. malmesburiensis,* currently recognized and *G. marlothii, G. rubicunda, G. ixioides, G. lewisiae, G. montana,* here reduced to synonymy.

During this time the artificially constituted genus *Acidanthera* was largely disassembled by Lewis (1941). Species were shown to belong to *Gladiolus, Hesperantha, Tritonia,* and *Geissorhiza* while a few, regarded by Lewis as allied to *Geissorhiza,* were assigned to a new genus *Engysiphon.* The criteria she used for distinguishing this genus from *Geissorhiza* are: unilateral and declinate stamens and style; filaments exceeding anthers; bracts firm throughout; and a long flower, usually with a well-developed perianth tube. Critical analysis shows that *Engysiphon* has no significant characters or character combinations not found in *Geissorhiza.* The genus is reduced to sectional subgeneric rank here.

The extensive botanical exploration of the higher Cape mountains, undertaken by Elsie Esterhuysen, began in the 1940s. Esterhuysen's Cape mountain collections, supplemented by those of Thomas Stokoe, Peter Jackson, and Ernest Galpin have brought to light a whole range of montane species of *Geissorhiza* and expanded the ranges of several more. As a result, *G. alticola, G. nubigena, G. esterhuyseniae, G. stenosiphon, G. scopulosa, G. unifolia, G. elsiae,* and *G. grandiflora,* previously unknown or poorly collected, were discoverd and are described here, while species such as *G. burchellii* and *G. ramosa* previously known only from one or a few gatherings from isolated mountain localities are now known to have extensive ranges. The high mountain species are still relatively poorly known, and it seems likely that novelties will continue to be discovered in the mountains of the western and southern Cape.

SYSTEMATIC TREATMENT

Geissorhiza Ker, Ann. Bot. (König & Sims) 1: 223. 1804; Baker, Handb. Irid. 152–159. 1802, Fl. Cap. 6: 65–76. 1896; Klatt, Abh. Naturf. Ges. Halle 15: 390–393 (Erg. 56–61). 1882; Durand & Schinz, Consp. Fl. Afric. 5: 176–181. 1895; Foster, Contr. Gray Herb. 135: 3–78. 1941; Lewis, Fl. Cape Penins. 252–256. 1950. TYPE: *G. obtusata* Ker [= *G. imbricata* subsp. *bicolor* (Thunb.) Goldbl.].

Ixia L. sensu L. f., Suppl. Pl. 91–94. 1782; sensu Thunb., Diss. de *Ixia* 1783, pro parte.

Weihea Ecklon, Topogr. Verz. Pflanzensamml. Ecklon 22. 1827, nom. nud.

Sphaerospora Klatt, Linnaea 32: 725. 1863, hom. illeg.

non Sweet ex Loudon (1841). TYPE: *S. exscapa* (Thunb.) Klatt (lectotype here designated).

Acidanthera Hochst. sensu Baker, Fl. Cap. 6: 130–134. 1896, pro parte.

Engysiphon Lewis, J. S. African Bot. 7: 19–24. 1941. TYPE: *E. schinzii* (Baker) Lewis (lectotype here designated, type not indicated by Lewis).

Plants small to medium in size. *Rootstock* a tunicate corm, with hard and woody to membranous, or rarely fibrous coverings, either asymmetric with one side flattened below and sometimes extending downwards shortly or evidently symmetric, but usually with the roots developing from a small ridge on one side; *tunics* either concentric (subgenus *Weihea*) with the outer layers usually light brown and completely enclosing the inner, fragmenting into irregular to elliptic segments, often drawn into points above and below; or imbricate (subgenus *Geissorhiza*) with the outer layers dark brown to blackish and covering the inner above only, regularly V-notched below into nearly rectangular segments. *Leaves* several to only 2 (rarely solitary), at least the lowermost basal and usually largest, decreasing in size above and the uppermost often becoming bract-like and entirely sheathing, erect to falcate or sometimes prostrate, linear, ensiform or linear; surface plane and smooth (rarely pubescent, *G. pusilla*), or with the margins and midrib raised and thus 2-grooved on each surface, sometimes (section *Ciliata*) the margins held at right angles to the blade and ciliate along the edges and the midrib (and occasionally other veins) raised and winged, with cilia along the edges, or lamina 3 to several ribbed and grooved (section *Geissorhiza*); margins smooth, ciliate to pubescent, or sticky and with adhering soil. *Stem* erect, terete, simple or branched and then either from the base or from cauline nodes. *Spike* usually several to many flowered, or sometimes only 1- or 2-flowered; always drooping in bud and becoming erect as the flowers open; *bracts* herbaceous to membranous, sometimes reddish on the upper margins, dry and brownish in the upper half (especially sections *Planifolia* and *Ciliata*), the outer larger and usually slightly longer than the inner, the inner bifid at the apex. *Flower* actinomorphic and stellate to hypocrateriform or zygomorphic with decumbent, declinate filaments and upright, unilateral anthers and a declinate style, variously colored with shades of purple and pink, or deep violet to blue most common, but also red, white, or yellow, the tepals often darker colored on the reverse and frequently reddish when flowers a pale color; *perianth tube* straight, shorter or about as long as the bracts, less often much longer than the bracts, usually cylindric; *tepals* oblong to obovate, the outer usually somewhat larger than the inner, spreading equally or with the posterior tepals upright and the anterior tepals horizontal and lying below the decumbent stamens and style. *Filaments* inserted near the top of the perianth tube, occasionally in lower part of the tube, erect and symmetrically disposed to unilateral and declinate, all equal or one consistently shorter than the other two (especially subgenus *Geissorhiza*); *anthers* oblong to linear, shortly tailed, subbasifixed, extrorse when symetrically disposed, well-exserted (included in section *Includanthera*), pollen yellow, blue, or violet. *Ovary* ovoid, style slender, initially erect, usually becoming displaced laterally or declinate and lying under the filaments, usually well-exserted and branching near the apex of the anthers, occasionally entirely included (section *Includanthera*), sometimes dividing at the mouth of the tube or at the base of the anthers, style branches usually short, ascending and ultimately recurved, occasionally flat and broadly lobed. *Fruit* a globose to obovoid capsule, usually about as long as the bracts; seeds globose to angular, light to dark brown. *Basic chromosome number*, $x = 13$.

Eighty-one species, restricted to the winter rainfall areas of southern Africa, and concentrated in the southwestern Cape; one species extending into northern Namaqualand and another into the eastern Karoo and Eastern Cape as far east as Cradock and Grahamstown.

KEY TO THE SPECIES OF *GEISSORHIZA*

1a. Stamens and style entirely included in perianth, not visible without opening the tube.
2a. Leaves plane, 3–5 mm wide; flowers white ..... 23. *G. esterhuyseniae*
2b. Leaves with margins and midrib heavily thickened, 1.5–2 mm wide; flowers pale pink with darker markings at base of tepals ..... 24. *G. cedarmontana*
1b. Stamens and style (or at least style branches) fully exserted from perianth tube.
3a. Leaf solitary, sheathing below, and with a membranous sheathing bract in upper part of stem ..... 32. *G. unifolia*
3b. Leaves two or more in addition to any entirely sheathing membranous to submembranous bracts in upper part of stem.
4a. Leaves spirally twisted and flowering stems single flowered.
5a. Flowers yellow with perianth tube to 3 mm long ..... 19. *G. corrugata*
5b. Flowers purple with perianth tube 4–5 mm long ..... 20. *G. spiralis*
4b. Leaves erect to falcate, not spirally twisted and flowering stems 2–several (rarely 1-flowered).
6a. Stem minutely ciliate, puberulent or pilose, partly or throughout.
7a. Stamens unequal, one at least 0.5 mm, but usually more than 1.5 mm shorter than the other two.
8a. Leaf more or less plane (margin and midrib sometimes slightly thickened).
9a. Stamens unilateral and declinate; flower large ..... 70. *G. monanthos*
9b. Stamens symmetrically disposed.
10a. One filament slightly shorter (less than 2 mm), tepals 11–16 mm long ..... 68. *G. aspera*
10b. One filament at least 4 mm shorter than other two, tepals 18–23 mm long ..... 69. *G. inaequalis*
8b. Leaf with margins and midrib raised significantly.
11a. Plant with 3 leaves and a small sheathing membranous bract in upper third whether branched or not from this point.
12a. Tepals 8–9 mm long; anthers 2–2.5 mm long ..... 65. *G. scopulosa*
12b. Tepals 10–22 mm long; anthers 4–6 mm long ..... 76. *G. heterostyla*
11b. Plant with 3 leaves but without a stem bract, whether branched or not.
13a. Leaves conspicuously ciliate-pubescent on the edges of the margins and midrib ..... 81. *G. leipoldtii*
13b. Leaves smooth or minutely ciliate along margins or midrib ..... 77. *G. arenicola*
7b. Stamens equal.
14a. Leaf plane.
15a. Tepals 14–22 mm long; stamens usually unilateral and declinate.
16a. Flower dark blue, sometimes red or pale in center ..... 70. *G. monanthos*
16b. Flower white, marked red to brown in center ..... 71. *G. tulbaghensis*
15b. Tepals 9–15 mm long; stamens symmetrically disposed ..... 68 *G. aspera*
14b. Leaf not plane, margins and midrib significantly raised.
17a. Margins extended at right angles to lamina and hispid to ciliate along edges; midrib and sometimes other veins also hispid to ciliate.
18a. Perianth tube short, to 4 mm long.
19a. Flower small, tepals 8–12 mm long; anthers 2.5–3 mm long ..... 80. *G. erubescens*
19b. Flower medium to large, tepals (13–)15–28 mm long; anthers (3–)6–8 mm long.
20a. Flower deep violet blue; stamens declinate; anthers brown ..... 78. *G. splendidissima*
20b. Flower white to pale purple; stamens symmetrically disposed; anthers yellow ..... 81. *G. leipoldtii*
18b. Perianth tube long, at least 6 mm and to 25 mm long.
21a. Perianth tube about as long as the bracts, 6–8(–11) mm long ..... 72. *G. namaquensis*
21b. Perianth tube much longer than bracts, 18–25 mm long ..... 73. *G. kamiesmontana*
17b. Margins and other veins not hispid or ciliate.
22a. Flower small, tepals 6–7 mm long; leaf to 1 mm wide ..... 66. *G. ciliatula*
22b. Flower medium-sized, tepals 7–10 mm long; leaf 1.5–3.5 mm wide ..... 31. *G. intermedia*

6b. Stem smooth.
23a. Stamens unequal, one at least 0.5 mm and usually more than 2 mm shorter than other two.
24a. Leaf margins winged and ciliate to hispid along the edges ..... 76. *G. heterostyla*
24b. Leaf margins either not winged, or if thickened to winged then not ciliate to hispid along the edges.
25a. Flower small, tepals 8–11 mm long.
26a. Stem erect, 2–3-branched (rarely simple); spike with up to 11 flowers; leaves with thickened margins and midribs; flowers usually purple to violet ..... 63. *G. ramosa*
26b. Stem usually inclined to trailing, occasionally with 1(–2) branches; spike usually 2–6-flowered; leaves flat or nearly so; flowers white ..... 64. *G. bryicola*
25b. Flower medium to large, tepals (12–)14–30 mm long.
27a. Flower cream to yellow, with or without dark markings in the center.
28a. Leaf few ribbed and grooved, or leaf nearly terete with narrow longitudinal grooves; flower yellow throughout ... 53. *G. louisabolusiae*
28b. Leaf several ribbed and grooved; flower yellow with dark markings in the throat ..... 52. *G. barkerae*
27b. Flower shades of blue, purple, or pink (rarely white).
29a. Perianth tube short, 2–3 mm long ..... 62. *G. tabularis*
29b. Perianth tube at least 4 mm and to 22 mm long.
30a. Leaves plane ..... 67. *G. pseudinaequalis*
30b. Leaf margins and midribs thickened.
31a. Tube 4–6 mm long ..... 60. *G. burchellii*
31b. Tube 10–22 mm long ..... 61. *G. grandiflora*
23b. Stamens equal.
32a. Leaves more or less plane (margins and midrib sometimes slightly thickened).
33a. Flower zygomorphic with stamens unilateral and declinate.
34a. Flower pink, large, tepals 22–32 mm long.
35a. Corm tunics soft textured, decaying readily; plants unbranched and trailing; perianth tube 10–13 mm long ..... 4. *G. outeniquensis*
35b. Corm tunics hard and woody, persistent; plants sometimes branched and erect; perianth tube 8–10 mm long ..... 3. *G. roseoalba*
34b. Flower purple, medium in size, tepals 12–15 mm long ..... 21. *G. karooica*
33b. Flower actinomorphic with stamens symmetrically disposed.
36a. Leaves linear to ensiform, narrow, 1–2(–3) mm wide, and never pubescent; stems 1–2-flowered.
37a. Perianth tube 6–8 mm long, typically exserted from the bracts; flowers white to cream, rarely pale yellow.
38a. Plants usually dichotomously branched, more than 12 cm high ..... 14. *G. geminata*
38b. Plants rarely branched but if so then not dichotomously, 4–8 cm high ..... 11. *G. setacea*
37b. Perianth tube 2–5 mm long; flowers white, yellow (often fading to greyish black), or pale lilac.
39a. Flowers in shades of yellow.
40a. Flowers stellate, with tepals 6–12(–18) mm long; perianth tube 2–3 mm long ..... 12. *G. ornithogaloides*
40b. Flowers cupped, with tepals 13–25 mm long; perianth tube 4 mm long ..... 13. *G. malmesburiensis*
39b. Flowers white or lilac.
41a. Perianth tube 3–5 mm long ..... 9. *G. bracteata*
41b. Perianth tube 1–3 mm long.
42a. Tepals 3–6 mm long, tube 1–2.5 mm long ..... 10. *G. nana*
42b. Tepals 6–12 mm long; tube 2–3 mm long ..... 8. *G. delicatula*
36b. Leaves ovate, ensiform or lanceolate, (2–)3–10 mm wide, smooth or pubescent; stems (1–)3–10-flowered.
43a. Lower leaves prostrate or inclined towards the ground.

44a. Flower large, tube 10–18(–30) mm long, as long or longer than the tepals 7–13 mm ..... 18. *G. ovata*
44b. Flower small to medium in size, tube to 8 mm long, shorter than the tepals.
45a. Spikes all single flowered; flowers pale lilac ..... 8. *G. delicatula*
45b. Spikes typically bearing more than a single flower; flowers white, cream, or pale yellow.
46a. Plants with cormlets produced in the axils of one or more leaves; leaves flaccid, usually more than 2 cm.
47a. Stem usually without or with only one cauline leaf or bract; flowers fertile and capsules developing rapidly after blooming ..... 15. *G. ovalifolia*
47b. Stem usually with 2 to several cauline leaves or bracts, all bearing axillary cormlets; flowers sterile and cormlets produced in place of capsules after flowering ..... 16. *G. bolusii*
46b. Plants without cormlets in the leaf axils; leaves firm, 1.5–2(–4.5) cm long ..... 17. *G. parva*
43b. All leaves erect to falcate.
48a. Perianth tube less than 3 mm long; flowers in shades of blue and purple.
49a. Leaves pubescent, at least below; bracts dry and brown in the upper half ..... 22. *G. pusilla*
49b. Leaves smooth entirely; bracts not dry and brown in the upper half ..... 7. *G. nigromontana*
48b. Perianth tube 3–6 mm long; flowers white or blue to purple.
50a. Perianth tube more than 7 mm long ..... 2. *G. elsiae*
50b. Perianth tube 2–6 mm long.
51a. Spike typically 3–7-flowered; perianth tube 4–6 mm long.
52a. Leaves 5 to several, lanceolate, less than a third of the length of the stem; tepals 13–17 mm long ..... 6. *G. foliosa*
52b. Leaves 3–5, ensiform to linear, one to two-thirds the length of the stem; tepals 8–11(–15) mm long ..... 1. *G. inconspicua*
51b. Spike typically 1(–3)-flowered; perianth tube 3–5 mm long ..... 9. *G. bracteata*
32b. Leaves not plane, either terete or nearly so, or margins and or other veins thickened or raised significantly.
53a. Outer floral bracts 15–65 mm long and the inner bracts about half as long as the outer.
54a. Leaves linear to terete, with the margins having raised wings curving over the inconspicuous midrib.
55a. Tepals nearly linear, acute and 3–4.5 mm wide ..... 46. *G. tenella*
55b. Tepals lanceolate to obovate, acute to obtuse and 4.5–11 mm wide.
56a. Perianth tube 15–30 mm long ..... 45. *G. bonae-spei*
56b. Perianth tube 40–80 mm long ..... 47. *G. exscapa*
54b. Leaves ensiform to linear or falcate, with the margins and midrib strongly thickened, the blade thus appearing broadly 2-grooved on each surface.
57a. Tepals 17–27 mm long, white or flushed with pink ..... 43. *G. longifolia*
57b. Tepals 28–40 mm long, pink or ivory yellow.
58a. Tepals usually longer than the tube, and 9–15 mm wide ..... 42. *G. schinzii*
58b. Tepals shorter than the tube, and 7–10 mm wide ..... 44. *G. confusa*
53b. Outer floral bracts 6–20(–25) mm long, and the inner bracts about as long, or only slightly shorter (at least two-thirds as long as outer).
59a. Leaves terete or nearly so, narrowly 4–(5–6)-grooved in section.
60a. Sheath of upper leaf conspicuously inflated and several ribbed and grooved.
61a. Perianth tube 3–4.5 mm long.
62a. Flower deep yellow, campanulate ..... 53. *G. louisabolusiae*
62b. Flower creamy white, stellate ..... 55. *G. sulphurascens*
61b. Perianth tube 5–9 mm long ..... 54. *G. brehmii*
60b. Sheath of upper leaf not inflated or conspicuously ribbed and grooved.
63a. Perianth tube well developed, (8–)12–50 mm long; stem simple or branched and then all axes single flowered.

64a. Tube 40–50 mm long; tepals 12–14 mm long ..... 35. *G. stenosiphon*
64b. Tube 8–20 mm long; tepals 20–30 mm long ..... 5. *G. fourcadei*

63b. Perianth tube short, 2–5 mm long; stem usually simple and 2 to several flowered.
65a. Flower small, tepals 8–12(–14) mm long; perianth tube 2–3 mm long; flower cream to pale yellow and not turning black when dry ..... 33. *G. juncea*
65b. Flower medium to large, tepals 15–22 mm long; perianth tube (3–)4–5 mm long; flower deep yellow and eventually turning black when dry ..... 34. *G. furva*

59b. Leaves not terete, surface either several ribbed or margins and midrib thickened or raised and the blade 2-grooved on each side; sometimes ciliate to pubescent along the edges of the ribs (edges of the margin and midrib sometimes wing-like).
66a. Stigmas broad and flat, 3–4 mm long and at least 2 mm wide.
67a. Perianth tube 6–9 mm long ..... 57. *G. eurystigma*
67b. Perianth tube 1–2.5 mm long ..... 58. *G. mathewsii*

66b. Stigmas slender, recurving and not noticeably ciliate.
68a. Bracts herbaceous to membranous, sometimes dry above but if so not brown-ferrugineous in the upper half.
69a. Perianth tube (8–)9–11 mm long.
70a. Flower yellow with a dark center; perianth tube longer than the bracts; stamens erect and symmetrically disposed ..... 28. *G. darlingensis*
70b. Flower pink to purple; perianth tube not reaching to the apex of the bracts; stamens unilateral and declinate ..... 41. *G. brevituba*

69b. Perianth tube 2–8 mm long.
71a. Tepals 5–25 mm long; leaves 2 or 3, and if 3, then the uppermost small and often becoming bract-like, sheath not inflated or several ribbed and grooved.
72a. Flower with a perianth tube 1–7(–8) mm long.
73a. Flowers small with the tepals 7–9 mm long and the tube 1–3(–3.5) mm long.
74a. Plants with 2 green produced leaves, the upper of these basal, long but sheathing the stem to at least the middle and with a short free apical part; stem bearing a short, 7–12 mm long, entirely sheathing, obtuse bract below the spike ..... 49. *G. scillaris*
74b. Plants with 2–3 green produced leaves, the second of these sheathing the stem for a short distance and usually shorter than the basal leaf; third leaf, if present, green and only partly sheathing with a free apex and the stem without a sheathing bract below the spike.
75a. Perianth tube ca. 1 mm long; the corm tunics hard, woody and blackish, the layers imbricate, and V-notched below ..... 56. *G. minuta*
75b. Perianth tube 2.5–3.5 mm long; the corm tunics soft, membranous and light brown, the layers evidently concentric ..... 30. *G. pappei*

73b. Flowers medium to large with the tepals 10–22 mm long and tube 2–10 mm long.
76a. Bracts sticky and with adhering sand.
77a. Flower large, usually clear yellow, tepals 16–22 mm long ..... 27. *G. humilis*
77b. Flower smaller, cream to pale yellow usually with red markings on the reverse of the outer tepals, tepals 10–15 mm long ..... 29. *G. hispidula*

76b. Bracts not sticky.
78a. Corm tunics either woody to firm and composed of distinct layers, the outer becoming broken, usually drawn into short points above.
79a. Flowers white and with a perianth tube 2.5–3 mm long and tepals 9–12 mm long and 5–6 mm wide ..... 48. *G. similis*

79b. Flowers purple and with a perianth tube 3–8 mm long and tepals 10–20 mm long and 6–9 mm wide.
80a. Perianth tube 3–6 mm long; spike 4–10-flowered ..... 26. *G. purpurascens*
80b. Perianth tube 7–8 mm long; spike 1–4-flowered ..... 25. *G. lithicola*

78b. Corm tunics either fibrous or composed of soft membranous layers, seldom accumulating, or the outer becoming fibrous.
81a. Perianth tube 2–4.5 mm long and the tepals less than 13 mm long.
82a. Flowers white and with a perianth tube 2.5–4 mm long; usually 2 long leaves produced and the third mostly sheathing and bract-like ..... 36. *G. umbrosa*
82b. Flowers purple and with a perianth tube 2–3 mm long; only the basal leaf produced and the other 2 or 3 mostly sheathing and bract-like with short free apices ..... 37. *G. alticola*
81b. Perianth tube 5–10 mm long, if less then the tepals at least 14 mm long.
83a. Flowers blue-purple to violet and the tube 5–8(–10) mm long; bracts ca. 10 mm long ..... 38. *G. hesperanthoides*
83b. Flowers pale bluish with a pale center and the tube 4–6 mm long; bracts 6–9 mm long ..... 39. *G. cataractarum*

72b. Flower with a perianth tube more than 8 mm and to 18 mm long.
84a. Perianth tube 10–18 mm long, well-exserted from the bracts at anthesis; tepals 17–22 mm long, pink to pinkish purple ..... 40. *G. nubigena*
84b. Perianth tube 5–8(–10) mm long, not or barely exserted from the bracts at anthesis; tepals 12–18 mm long, blue-purple to violet ..... 38. *G. hesperanthoides*

71b. Tepals at least 10 mm long and leaves 3, with the uppermost large and with an inflated, several ribbed and grooved sheath.
85a. Tepals white to yellow, with or without a dark purple to brown center; without a pit in the midline of the tepals.
86a. Flowers with the tepals cupped when fully open ..... 53. *G. louisabolusiae*
86b. Flowers with the tepals spread horizontally when fully open.
87a. Lower two leaves filiform and with only the margins and midrib thickened.
88a. Plants short, 4–12(–17) mm high; spike 1–3(–5)-flowered; flowers often with a dark center ..... 51. *G. purpureolutea*
88b. Plants medium to tall, to 12–20 mm high; spike 4–10-flowered; flowers cream to pale yellow throughout ..... 55. *G. sulphurascens*
87b. Lower two leaves linear, with the margins and two or more other veins thickened.
89a. Perianth tube 2–8 mm long, but if only 2–4 mm then the flower not dark in the center ..... 50. *G. imbricata*
89b. Perianth tube 2–4 mm long and the flower dark in the center ..... 51. *G. purpureolutea*
85b. Tepals deep purple with white and red markings with a conspicuous pit in the midline ..... 59. *G. radians*

68b. Bracts dry and brown-ferrugineous at least in the upper half at flowering time.
90a. Plants with 3 green leaves, and lacking bracts below the spike ..... 79. *G. inflexa*
90b. Plants with 3 green leaves, and bearing 1 or 2 dry sheathing bracts below the spike.
91a. Tepals ca. 10 mm long ..... 74. *G. divaricata*
91b. Tepals 12–17 mm long ..... 75. *G. subrigida*

NOTE ON CITATION OF SPECIMENS AND SPECIMEN PRESERVATION

Specimens examined are arranged according to the grid reference system based on geographical degree co-ordinates of latitude and longitude in current use in southern Africa (Edwards & Leistner, 1971). All type material cited was seen unless indicated to the contrary.

Descriptions are based on both fresh and the available dried material but measurements are based on living plants. A shrinkage factor of 10% or more may be expected for leaves and flower parts, depending on the care and method of preservation. Flower color fades progressively in dry specimens, eventually changing completely, becoming darker and sometimes ultimately disappearing. Color notes on collected specimens are desirable and are frequently mentioned by collectors.

SUBGENUS *WEIHEA*

1. Subgenus **Weihea** (Ecklon ex Baker) Goldbl., stat. nov. *Geissorhiza* section *Weihea* Ecklon ex Baker, J. Linn. Soc., Bot. 16: 95. 1878; Foster, Contr. Gray Herb. 135: 39. 1941. *Weihea* Ecklon, Topogr. Verz. Pflanzensamml. Ecklon 22. 1827, nom. nud. TYPE: *Geissorhiza ovata* (Burm. f.) Asch. & Graeb. [as *G. excisa* (Thunb.) Ker, lectotype effectively designated by Foster (1941)].

Corms with concentric, brownish tunics, *leaves* lanceolate to ensiform or linear, and blade plane, or with the margins and midrib thickened, then sometimes terete, smooth rarely ciliate-pubescent, *stem* smooth, rarely ciliate, *spike* 1 to several flowered, *bracts* herbaceous, sometimes becoming dry above, rarely ferrugineous, *flowers* hypocrateriform, stellate or declinate, tube about as long as the bracts, or very short, or extremely long (section *Engysiphon*), stamens equal, rarely included in the tube.

Species. 47.
Distribution. Figure 6.

SECTION *WEIHEA*

1. Section **Weihea.** TYPE: *G. ovata* (Burm. f.) Asch. & Graeb.

Geissorhiza subsection *Foliosae* Foster, Contr. Gray Herb. 135: 55. 1941. TYPE: *G. foliosa* Klatt, nom. superfl. pro subsection *Weihea.*

Corm tunics woody to firm or soft in texture, leaves lanceolate to ensiform or linear, blade plane, smooth, occasionally terete and 4-grooved, *stem* smooth, *spike* 1 to several flowered, *bracts* herbaceous, rarely becoming dry above, *flowers* hypocrateriform or declinate, tube about as long as the bracts, or to about twice as long.

Species. 18.

1. Geissorhiza inconspicua Baker, Kew Bull. 1906: 26; Foster, Contr. Gray Herb. 135: 65–66. 1941. TYPE: South Africa. Cape: George, Montagu Pass, *Penther 713* (holotype, K). FIGURE 19.

Geissorhiza violacea Baker, Kew Bull. 1906: 26. 1906; Foster, Contr. Gray Herb. 135: 61. 1941. TYPE: South Africa. Cape: Knysna, "Blau Krantz" River, *Penther 677* (holotype, K).

Plants 10–18(–30) cm high. *Corm* globose, asymmetric with an obliquely flattened side extending downward shortly, 5–8 mm diam., tunics concentric, dark brown, outer layers sometimes becoming papery and soft, fragmenting irregularly into sections. *Cataphyll* pale, membranous, often evidently lacking. *Leaves* 3–5, usually erect, 2.5–6 mm wide, ensiform to linear, one to two-thirds as long as the stems, lower 2–3 basal, upper cauline and smaller, uppermost often bract-like. *Stem* erect, simple or more often 2–5-branched, both from base and upper stem nodes. *Spike* (1–)3–7-flowered; *bracts* 6–8 mm long, herbaceous, becoming membranous above and usually reddish along the margins, inner about as long as outer. *Flowers* stellate, either blue to purple (purple-pink when faded) or white to cream with pink on reverse of outer tepals; *perianth tube* 4–5(–6) mm long, cylindric, reaching nearly to the apex of the bracts; *tepals* 8–11(–15) mm long, obovate, 5–6 mm wide. *Filaments* 4–6(–8) mm long; *anthers* 3–4 mm long, pollen yellow. Ovary 2–3 mm long; *style* dividing at apex of anthers, branches ca. 2 mm long, recurved. *Capsule* obovoid, 5–7 mm long. *Chromosome number,* $2n = 26$ (*Vlok s.n.* no voucher, George).

Flowering time. (September to) October to November at low altitudes, occasionally to February at highest altitudes.

Distribution. From the Langeberg near Swellendam to Port Elizabeth, montane or on flats along the coast. Figure 19.

As circumscribed here, *Geissorhiza inconspicua* comprises forms with either white or blue- to purple-colored flowers. The type collection of *G. inconspicua* has white flowers and plants matching the type exactly. They occur in montane hab-

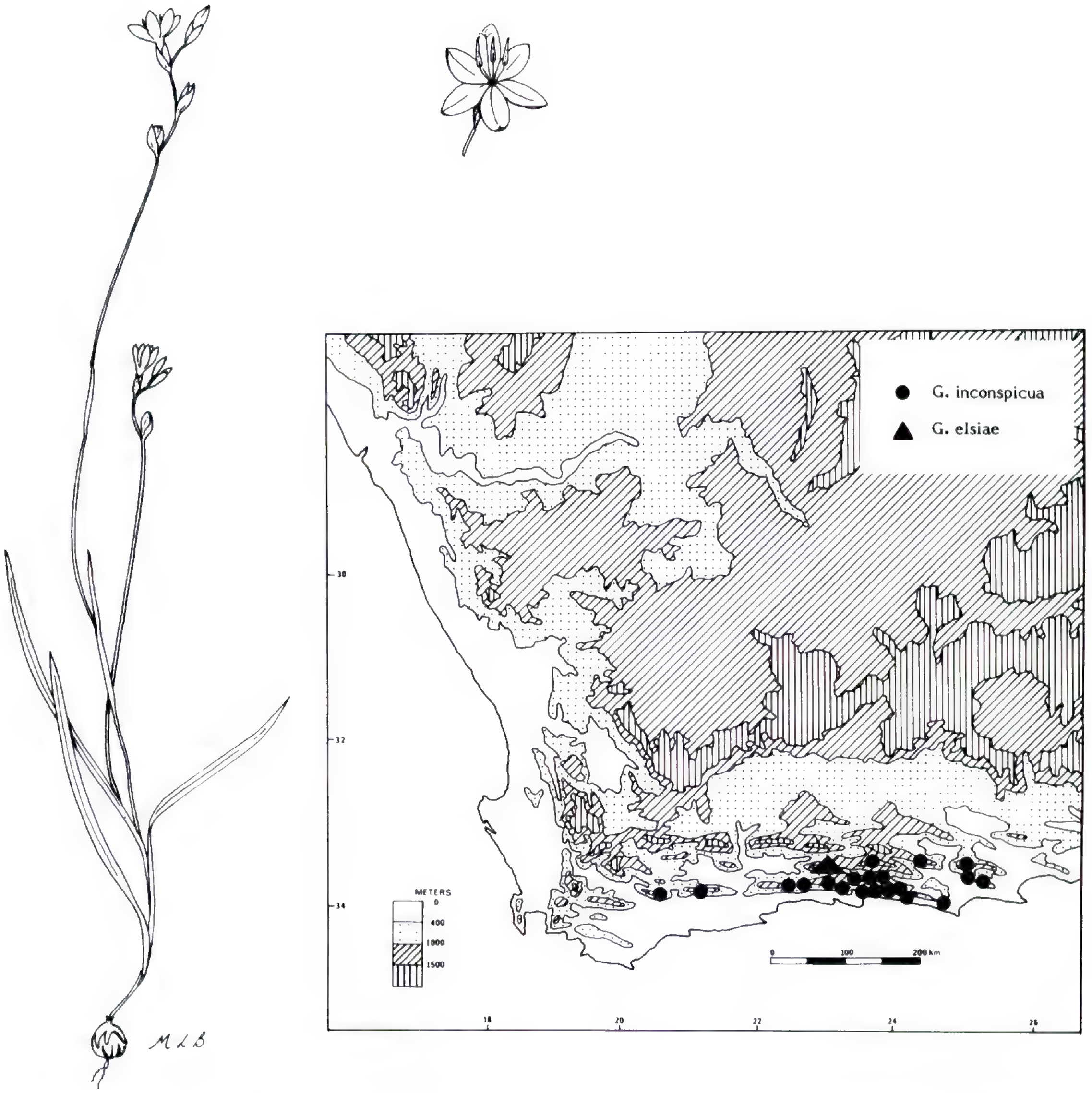


FIGURE 19. Morphology of *Geissorhiza inconspicua* and distribution of *G. inconspicua* and *G. elsiae*. Habit ×0.5; flower life size (*Vlok 515*, Baviaanskloof Mts.).

itats from Swellendam in the west to near Uitenhage in the east. In the center of its range, in the Tsitsikamma Mountains and along the adjacent coast, there is a blue- or purple-flowered form that matches in all respects the white-flowered plants except for the flower color. All the collections of this form, many of which comprise several individuals, are uniformly purple-flowered, which suggests that there is no intrapopulational variation for flower color. The purple-flowered plants appear to correspond to the type of *G. violacea*, a specimen in rather poor condition. Except for flower color it is impossible to distinguish specimens typical of *G. inconspicua* from the several collections of purple to bluish flowered plants, and *G. violacea* is here reduced to synonymy.

Geissorhiza inconspicua can usually be distinguished from other species of the genus by its rather short leaves clustered at the base of the plant and its typically well-branched stems with several flowered spikes held well above the leaves. It is closely related to *G. bracteata* which also has rather short leaves, but it differs in having spikes of 1–2 (rarely 3) flowers in contrast to the several usually found in *G. inconspicua*. How-

ever, smaller and fewer flowered specimens of *G. inconspicua* may be extremely difficult to distinguish from some individuals of *G. bracteata.*

Geissorhiza inconspicua can also be difficult to distinguish from the Langeberg species, *G. foliosa.* This species has distinctive, short and often relatively broad, lanceolate leaves in contrast to the longer, ensiform to linear leaves of *G. inconspicua.* In addition, *G. foliosa* usually has larger flowers than those of *G. inconspicua,* with tepals 13–17 mm long and anthers 4–6 mm long while in *G. inconspicua* the tepals are 8–11(–15) mm long and the anthers 3–4 mm long.

The species is probably very close to the ancestral stock of *Geissorhiza* and it has no characteristics that appear to be in any way specialized. It has probably persisted in the relatively temperate and well-watered southern Cape with very little change since at least the Pliocene.

Specimens examined. SOUTH AFRICA. CAPE: 3320 (Montagu) Tradouw Pass, 1,400 ft. (DC), *Wurts 2186* (NBG); Swellendam hiking trail, Langeberg Mts., *Esterhuysen 35605* (K, MO, PRE, S, US, WAG); 9 mi. from Barrydale on the road to Heidelberg, *Marsh 958* (K).

3321 (Ladismith) S end of Garcias Pass (CC), *Lewis 5641* (NBG); Garcias Pass (CC), *Thorne s.n.* (SAM 41607).

3322 (Oudtshoorn) Power Station above George (CD), *Gillett 2095* (BOL, STE); Montagu Pass, *Hutchinson 1216* (BOL, K), *Rehmann 63* (BM, BR, Z), *Schlechter 5796* (B, BM, BOL, BR, E, G, GH, K, PRE, S, UC, Z); Outeniqua Pass, *Barker 7657* (NBG), *Werdermann & Oberdieck 862* (B, K, PRE); S slopes of Tierkop, Outeniqua Mts., 1,500 m, *Vlok 356* (MO, SAAS); Hoogeberg, Knysna (DD), *Keet 977* (PRE), *1048* (PRE).

3323 (Willowmore) Kirby (CD), *Fourcade 6130* (STE), *6212* (BOL); 6 mi. E of Keurboom Strand, *Lewis 6166* (NBG); Kouga Mts., near Smutsberg (DA), *Esterhuysen 10772* (BOL, K, NBG, PRE); Lottering, Knysna Div. (DC), *Laughton 68* (BOL); Blaaukrantz Forest Reserve, *Middlemost 1805* (NBG, SAM); Bloukrans, *Barker 6050* (NBG); Helpmekaar Peak, 4,800 ft., S slopes, *Compton 4500* (NBG); De Hoek, near Joubertina, N foot of the Tsitsikamma Mts. (DD), *Esterhuysen 27317* (BOL, MO, PRE, US); slopes of the Tsitsikamma Mts., near Joubertina, *Esterhuysen 16757* (BOL), *13315* (BOL), *18349* (BOL, K); Elandsbosrivier, Tsitsikamma Park, *Bower 604* (PRE).

3324 (Steytlerville) Wit Els Berg (CC), *Esterhuysen 6786* (BOL); Cockscomb, Great Winterhoek Mts. (DB), *Esterhuysen 28009* (BOL).

3325 (Port Elizabeth) Van Stadens Mts., 1,500 ft. (CC), *Thompson 1862* (PRE); Blueberg, Loerie Forest Reserve, *Dix 55* (BOL).

3423 (Knysna) near Plettenberg Bay (BB), *Salter 6947* (BOL, STE), *Rodin 1175* (BOL, K, MO, PRE, UC); Smart sub *Rogers 27959* (Z); Keurbooms River (AB), *Schlechter 5949* (B, Z).

3424 (Humansdorp) Groot River, veld (AA), *Barker 6053* (NBG, STE); Baviaanskloof Mts., above the farm Enkeldoorn, 1,300 m (CB), *Vlok 515* (K, MO, SAAS).

LOCALITY UNCERTAIN: Blaaubosch Pass, S side, *Fourcade 2823* (BOL, K, STE); Ratelsbos flats, *Fourcade 352* (BOL).

2. Geissorhiza elsiae Goldbl., sp. nov. TYPE: South Africa. Cape: Kammanassie Mts., Mannetjiesberg, 4,000–5,000 ft., S slopes, *Esterhuysen 6412* (holotype, BOL; isotypes, BOL, K, PRE). FIGURE 1.

Planta 14–25 cm alta, foliis 4–5, basalibus lineare-ensiformibus planis, superiore caulem vaginanti, caule erecto, bracteam brevem ferenti, spica florum 2–4, floribus stellato-hypocrateriformibus purpureis, tubo 6–10 mm long, tepalis 15–20 mm longis, antheris 5–6 mm longis, stylo diviso prope apicem antherarum, ramis recurvatis.

Plants 14–25 cm high. *Corm* globose with one side flattened below, 7–10 mm diam., tunics concentric, dark brown. *Cataphyll* pale, membranous. *Leaves* (3–)4–5, erect to falcate, at least the lower 3 basal, (2–)3–6 mm wide, ensiform to linear, reaching to the base of the spike or only half to one-third as long as the stems, upper cauline and becoming smaller, sometimes uppermost bract-like. *Stem* erect, simple or branched from the upper 1–2 stem nodes. *Spike* 2–4-flowered; *bracts* 12–14 mm long, evidently herbaceous, becoming reddish above and on the veins, the inner usually shorter than the outer. *Flowers* stellate-hypocrateriform, purple with darker markings in the lower midline of the tepals (becoming colorless when dry); *perianth tube* 6–10 mm long, cylindric, initially reaching to about the apex of the tube, later shortly exserted; *tepals* 15–20 mm long, obovate, 7–8 mm wide. *Filaments* 6–11 mm long; *anthers* 5–6 mm long, pollen yellow. Ovary 2–3 mm long; *style* dividing at apex of anthers, branches to 3 mm long, recurved. *Capsule* 7–9 mm long, ovoid. *Chromosome number,* unknown.

Flowering time. Late October to mid-November.

Distribution. South slopes of the Kammanassie Mountains in the Little Karoo, in cool damp sites. Figure 19.

This species is known only from three collections made by Elsie Esterhuysen and recently by Jan Vlok, in the Kammanassie Mountains, an isolated range in the Little Karoo, lying between the coastal Outeniqua and interior Swartberg Mountains. It is clearly related to the more widespread *G. inconspicua,* which occurs along the

coastal Langeberg, Outeniqua and Tsitsikama ranges from Swellendam in the west to Uitenhage in the east. *Geissorhiza elsiae* can be distinguished from *G. inconspicua* by its larger flowers, 1–4-flowered spike and less branched habit, with the branches, when present, produced from the upper nodes rather than from near the base. It also bears some resemblance to *G. roseoalba,* which has a similar habit, but somewhat larger and zygomorphic, declinate flowers.

Specimens examined. SOUTH AFRICA. CAPE: 3322 (Oudtshoorn) Kammanassie Mts., near Laudina (DB), *Esterhuysen s.n.* (BOL); Mannetjiesberg, Kammanassie Mts., *Esterhuysen 6412* (BOL, K, PRE); S slopes of Mannetjiesberg in moss near waterfall, 5,100 ft., *Vlok 803* (MO).

3. **Geissorhiza roseoalba** (Lewis) Goldbl., comb. nov. *Acidanthera roseoalba* Lewis, S. African Gard. 23: 266. 1933. *Engysiphon roseoalbus* (Lewis) Lewis, J. S. African Bot. 7: 24. 1941. FIGURE 20. TYPE: South Africa. Cape: Doorn River, George, *Fourcade 4744* (holotype, BOL; isotypes, BOL "Herb. Fourcade," STE).

Plants 15–20 cm high. *Corm* globose, more or less asymmetric with an oblique flat side, 8–10 mm diam., tunics concentric, dark brown, woody, fragmenting irregularly into segments. *Cataphyll* pale, membranous, often evidently lacking. *Leaves* 3–5, erect to falcate, the lower 2–3 basal, the upper cauline and becoming smaller, sometimes uppermost bract-like, 3–6 mm wide, ensiform to linear, usually reaching to about base of spike or shorter. *Stem* erect, simple or 1-branched, from an upper node. *Spike* 1–3-flowered; *bracts* 14–18(–25) mm long, herbaceous, becoming membranous above and often reddish along the margins, the inner equal to or somewhat shorter than the outer. *Flower* zygomorphic, declinate, whitish inside with red markings near base of tepals, reddish on reverse of tepals; *perianth tube* 8–10 mm long, cylindric, initially not exserted from the tube, sometimes becoming shortly exserted later; *tepals* 22–32 mm long, oblong to obovate, 10–15 mm wide. *Filaments* equal, declinate, 12–20 mm long; *anthers* 6–8 mm long, pollen yellow. Ovary ca. 4 mm long, *style* dividing at the apex of the anthers, branches 3–4 mm long, recurved. *Capsule* unknown. *Chromosome number,* $2n = 26$ (*Vlok 706*).

Flowering time. August to September.

Distribution. Southern Cape in the Outeniqua, Kammanassie, Great Winterhoek, and Baviaanskloof Mountains. Figure 20.

Geissorhiza roseoalba was originally assigned to the artificially constituted genus *Acidanthera* when first described (Lewis, 1933). Shortly afterward, when Lewis (1941) reviewed this genus, she transferred *G. roseoalba* to the new genus *Engysiphon.* It differs markedly from the other species that were placed in *Engysiphon* in having three to five fairly soft-textured leaves with a plane lamina in contrast to the one to two firm leaves with heavily thickened and viscid margins of the remaining species of *Engysiphon,* now *Geissorhiza* section *Engysiphon.* It seems likely that *G. roseoalba* is not at all related to the species of section *Engysiphon* but is probably allied to the primitive *G. inconspicua* of subgenus *Weihea* section *Weihea.* It is accordingly assigned to this section where it stands out as being one of the largest flowered species in the alliance and one of the two in the section with a zygomorphic flower with declinate stamens and style.

Geissorhiza elsiae, a local endemic of the Kammanassie Mountains, is particularly reminiscent of *G. roseoalba,* and it is difficult to draw the line between the two species from dried material when the important details of the orientation of style and stamens are often not clear. *Geissorhiza elsiae,* however, has symmetrically disposed stamens and flowers that seldom reach the size of those of *G. roseoalba.*

Geissorhiza roseoalba is apparently restricted to dry fynbos and it extends from near Calitzdorp in the Little Karoo, eastwards through the Long Kloof and Baviaans Kloof to the Winterhoek Mountains near Uitenhage. It is poorly collected despite its fairly wide distribution and was only recently discovered in the Gamka Nature Reserve near Calitzdorp by J. J. Vlok and in the Uitenhage district by H. T. Scharf, significant range extensions for the species. It blooms from August in drier inland sites to late September in the higher rainfall areas towards the coast.

Specimens examined. SOUTH AFRICA. CAPE: 3321 (Ladismith) Gamka Nature Reserve, moist sandy S slopes (DA), *Vlok 318* (MO, SAAS); Attaquaskloof, Paardevlei Mts., 1,600 ft. (DD), *Vlok 706* (MO, SAAS).

3322 (Oudtshoorn) Doorn River, George (CC), *Fourcade 4744* (BOL, STE); between Doorn River and the top of Montagu Pass (CD), *Fourcade 5241* (PRE); farm Croxden, Waboomskraal, George, *O'Connor s.n.* (K, PRE); Buffelsrivier, SW of Kammanassieberg, 2,900 ft. (DA), *Oliver 3645* (K, PRE, STE).

3324 (Steytlerville) Baviaanskloof Mts., between

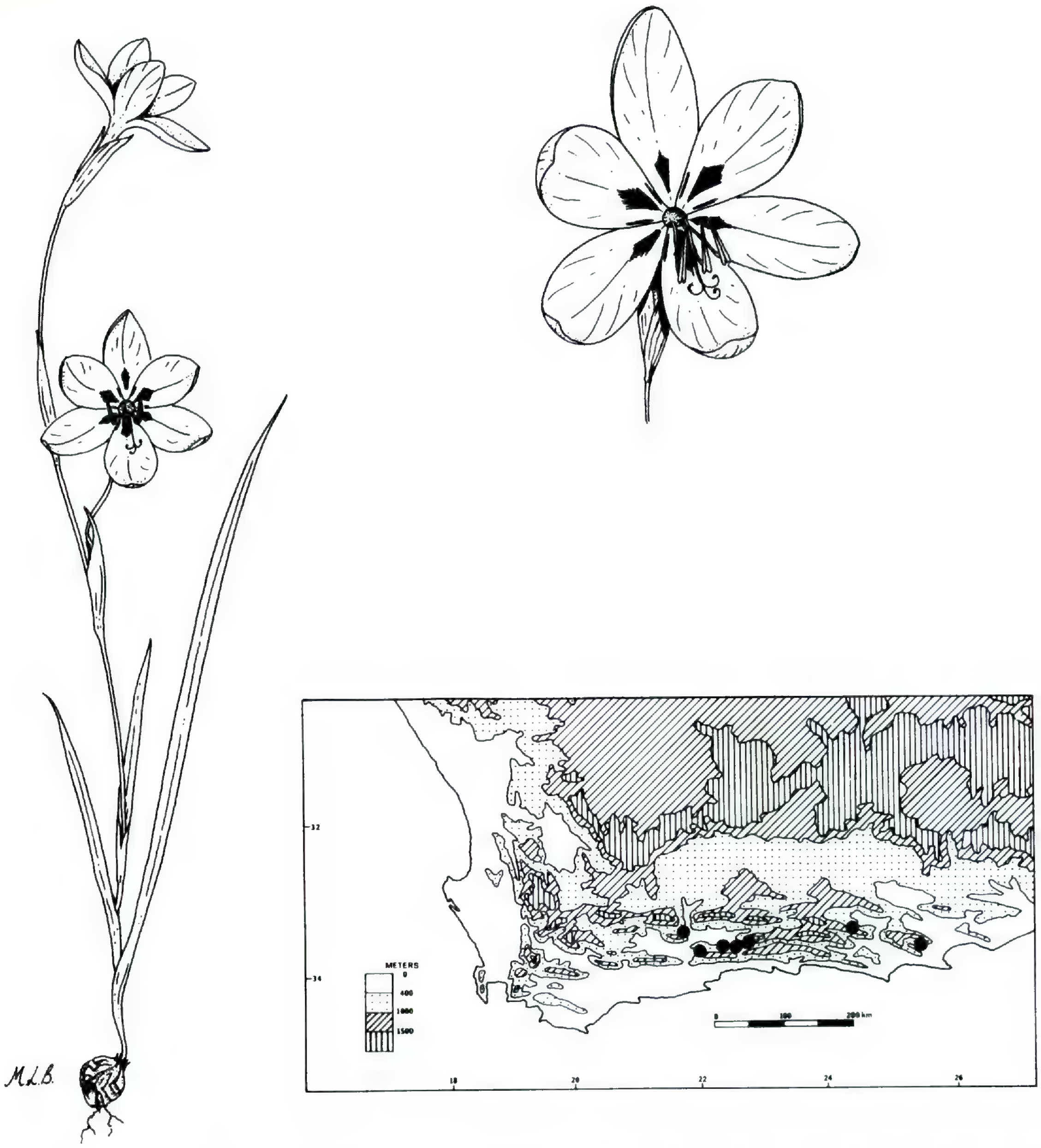


FIGURE 20. Morphology and distribution of *Geissorhiza roseoalba*. Habit ×0.5; flower life size (*Vlok 706*, Attaquaskloof).

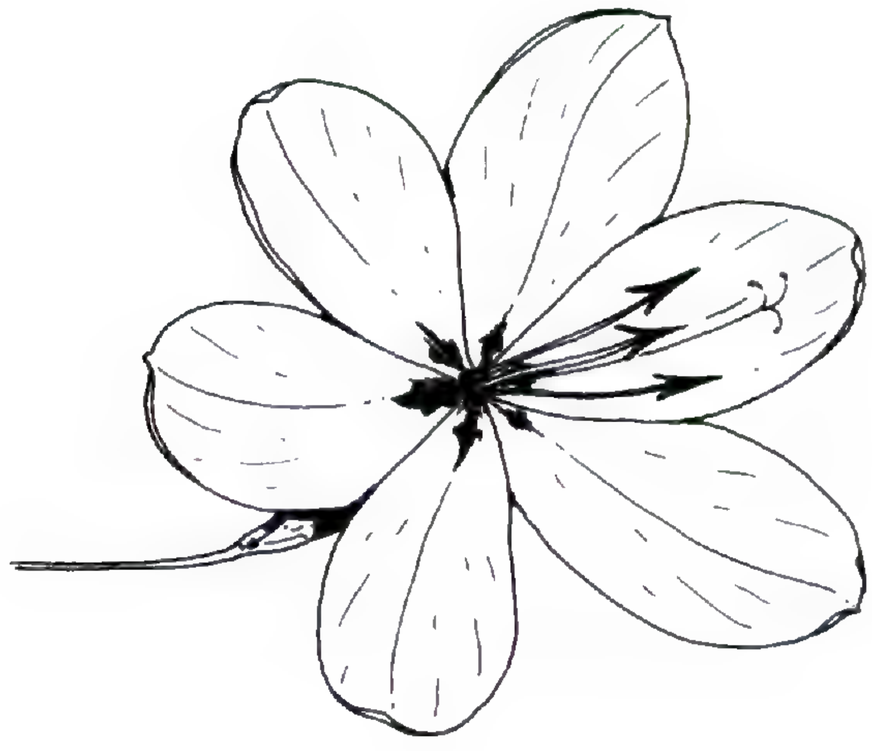
Smitskraal and Wilgehof, 3,500 ft. (CB), *Oliver 4586* (K, STE).

3325 (Port Elizabeth) Deysels Plaat farm, Groendal Wilderness Reserve (CA), *Scharf 1930* (PRE); Groendal Wilderness Reserve, Enon Conglomerate, on a burnt S-facing slope, *Scharf 1517* (PRE).

4. Geissorhiza outeniquensis Goldbl., sp. nov. TYPE: South Africa. Cape: George, Jonkersberg, Outeniqua Mts., wet rocky stream banks and waterfalls, *Esterhuysen 19379* (holotype, BOL; isotypes, K, PRE). FIGURE 21.

Planta 20–50 cm longa, caespitosa decumbenti, foliis 4-pluribus planis inferioribus basalibus superioribus caulem vaginante, caule decumbenti, spica florum 2–4, floribus hypocrateriformibus, carneis ad purpureis, tubo 10–13 mm longo, tepalis 26–32 mm longis, antheris 6–9 mm longis, stylo diviso propre apicem antherarum, ramis recurvatis.

Plants 20–50 cm long, usually decumbent or



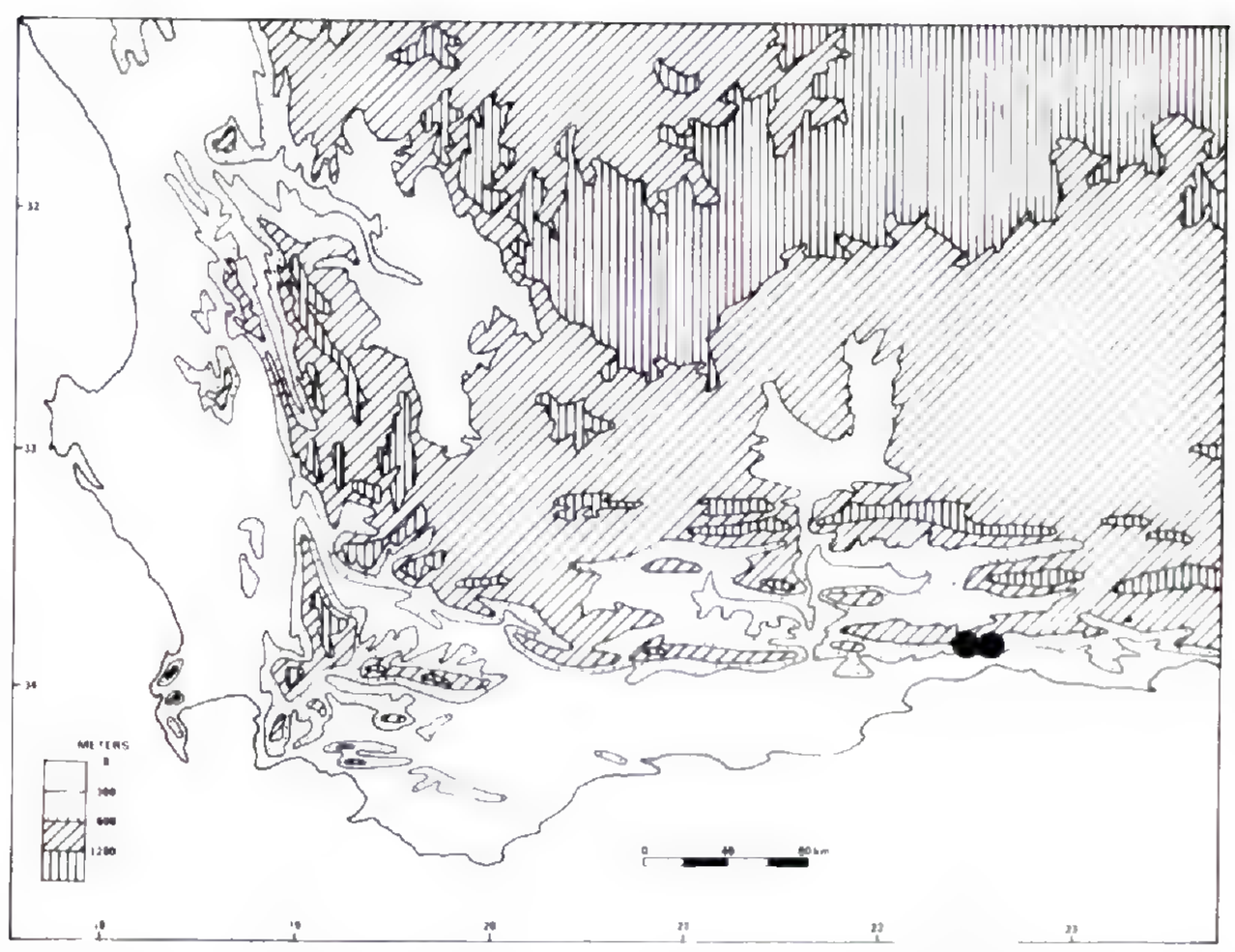


FIGURE 21. Morphology and distribution of *Geissorhiza outeniquensis*. Habit ×0.25; flower life size (*Vlok 525*, Outeniqua Pass).

trailing, forming clumps. *Corm* depressed-globose, symmetric, 6–8 mm diam., tunics apparently concentric, light brown, papery and soft, decaying readily. *Cataphyll* evidently lacking. *Leaves* 4 to several, decumbent to trailing, at least the lower two basal, upper cauline and becoming smaller and sometimes bract-like, 3–6 mm wide, linear, usually reaching to the base of the spike, sometimes longer. *Stem* decumbent, unbranched. *Spike* 2–4-flowered; *bracts* 16–20 (–24) mm long, herbaceous, becoming submembranous above, the inner slightly shorter than the outer. *Flower* zygomorphic, declinate, pink to purple with darker markings near the base of the lower tepals, purple on the reverse; *perianth tube* 10–13 mm long, cylindric, about as long or slightly longer than the bracts; *tepals* 26–32 mm long, oblong, 10–14 mm wide. *Filaments* equal, declinate, 15–20 mm long; *anthers* 6–8 mm long, pollen yellow. *Ovary* ca. 5 mm long, *style* dividing at the apex of the anthers, branches 3–4 mm long, recurved. *Capsule* unknown. *Chromosome number*, $2n = 26$ (*Vlok 525*).

Flowering time. December to mid-January.

Distribution. Local in the Outeniqua Mountains, in shady situations near water. Figure 21.

Geissorhiza outeniquensis has until now been considered a form of the more widespread *G. roseoalba,* which until recently was referred to the genus *Engysiphon.* It clearly belongs in section *Weihea* and seems closely related to *G. roseoalba.* These are the only two species of the section which have a zygomorphic flower with declinate stamens and style. They also have the largest flowers in the section and are so distinctive that they are unlikely to be confused with other species of the section. The flowers of *G. outeniquensis* are very similar to those of *G. roseoalba* but are normally slightly larger and have a longer perianth tube, some 10–13 mm long, compared to 8–10 mm in *G. roseoalba.* The very soft textured corm tunics of *G. outeniquensis,* however, are so different from those of *G. roseoalba* that the two species are unlikely to be confused.

Geissorhiza outeniquensis is apparently restricted to the Outeniqua Mountains immediately around George, where it occurs in moist shady kloofs, along streams and waterfalls. It has an unusual caespitose habit, with the main plants producing short runners which sprout to form new stems and leaf clusters. The species seems to have lost the deciduous habit of the genus, and does not die back and become dormant during the later summer and autumn.

Specimens examined. SOUTH AFRICA. CAPE: 3322 (Oudtshoorn) Jonkersberg, Outeniqua Mts., stream banks and waterfalls (CC), *Esterhuysen 19379* (BOL, K, PRE); Outeniqua Pass, streambanks and seepages (CD), *Acocks 21738* (B, K, NBG, PRE), *Vlok 525* (MO, NBG, PRE); "Geelhoutbosch," George, damp places, *Taylor 1628* (BOL); Montagu Pass, *McNeil & Ising s.n.* (PRE), *Zinn s.n.* (SAM 54823).

5. Geissorhiza fourcadei (L. Bolus) Lewis, J. S. African Bot. 7: 32. 1941. *Acidanthera fourcadei* L. Bolus, Ann. Bolus Herb. 4: 118. 1928. TYPE: South Africa. Cape: S slopes of Witte Els Berg, Humansdorp, *Fourcade 2968* (lectotype, BOL; isolectotypes, BOL "Herb. Fourcade," MO, PRE, S, STE). FIGURE 22.

Plants 15–30 cm high. *Corm* nearly spindle-shaped, 6–10 mm diam., corms of previous seasons persistent and accumulating below current corm, tunics brown, woody to soft-papery, layers concentric but sometimes apparently imbricate by displacement especially when soft, fragmenting irregularly from above and below, outer layers sometimes becoming fibrous, extending upward in a neck together with decaying leaves. *Cataphyll* membranous, light to dark brown. *Leaves* 3–5, terete or nearly terete, the margins and midrib actually much enlarged, and thus narrowly 4-grooved, half as long to as long as the stem, the lower 2–4 leaves basal, the uppermost cauline, partly to entirely sheathing, shortest. *Stem* erect, smooth, simple or 1–2-branched, bearing one partly sheathing foliage leaf and 2–3 dry sheathing stem bracts. *Spike* single flowered (both main and lateral axes); *bracts* herbaceous, drying near the apex, (12–)16–30 mm long, the inner as long, or slightly shorter than the outer. *Flower* hypocrateriform, pink to mauve; *perianth tube* (8–)17–20 mm long, cylindric, widening gradually towards the apex, exserted, or just short of the apex of the bracts; *tepals* 25–30 mm long, oblanceolate, to 11 mm wide. *Filaments* 13–20 mm long, equal; *anthers* 10–12 mm long. *Ovary* ca. 4 mm long, *style* declinate, dividing beyond the anthers, branches recurved. *Capsule* unknown. *Chromosome number,* unknown.

Flowering time. Mid-January to early May.

Distribution. Mountains of the southern Cape, in seasonally moist sites, such as seeps, streamsides, and marshes. Figure 22.

Geissorhiza fourcadei is distinctive in *Geissorhiza* in the persistent bases of leaves and cataphylls which accumulate in a neck around the stem base and in the spike and its branches always being single flowered. It is also peculiar in that the corms of past seasons often persist instead of decaying, so that a series of old corms accumulate behind the current year's corm. It is also unusual in its late summer to autumn blooming habit. The affinities of *G. fourcadei* are uncertain but the corm tunics correspond fairly well to the concentric type characteristic of subgenus *Weihea.* It seems isolated in the subgenus but is best placed in section *Weihea* in which there is a marked tendency to the reduction of the number of flowers in the spike. It stands out in the section in its terete 4-grooved leaf. Difficulties in placing the species to subgenus arise because the corm tunics are often soft in texture, sometimes even fibrous, and are then easily displaced from their concentric position when uprooted. The tunics then match neither the typical concentric tunics of subgenus *Weihea* nor correspond well with the imbricate tunics of subgenus *Geissorhiza.* The tunic layers of some collections, notably *Vlok 812,* are hard and perfectly concentric, and it seems clear that the tunics are basically concentric even though they are often easily displaced when disturbed.

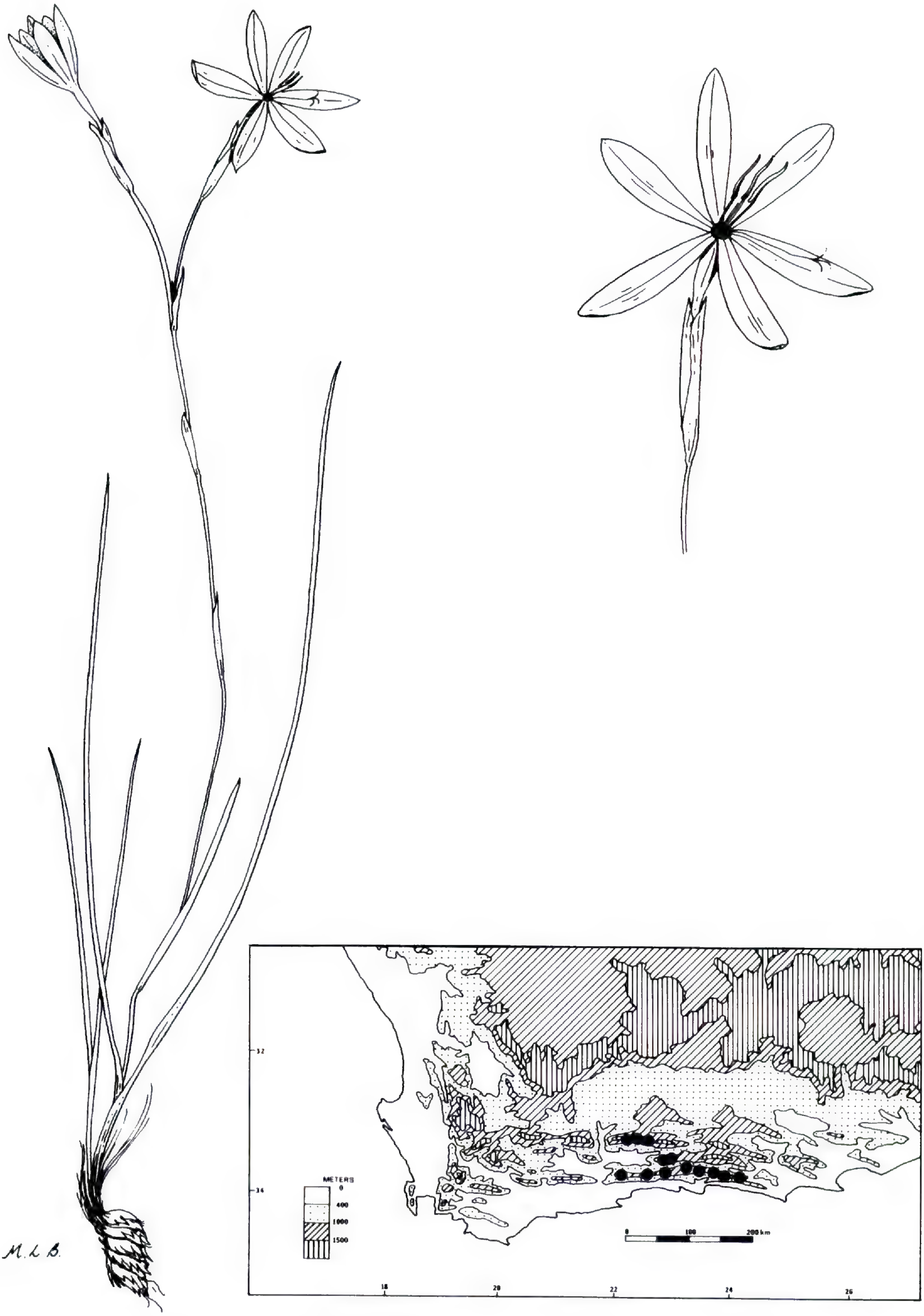


FIGURE 22. Morphology and distribution of *Geissorhiza fourcadei* (from dried plants and photographs). Habit ×0.5; flower life size (*Esterhuysen 4584*, Helpmekaar Peak).

Geissorhiza fourcadei occurs in sandy soils, probably always in damp situations, in the southern Cape mountains. It has been recorded from Robinsons Pass, at the western end of the Outeniqua Mountains almost to the eastern end of the Outeniqua-Tsitsikamma ranges at Witte Els Berg. Outlying populations have been recorded inland on the Kammanassie Mountains and at a few sites in the Swartberg Mountains to the north, between Meirings Poort and Swartberg Pass. A collection from the summit of Blouberg, *Thompson 2226,* stands out as having unusually short bracts (12–15 mm long) and perianth tube (ca. 8 mm long) but otherwise matches *G. fourcadei* well. It seems to represent nothing more than a depauperate population as other collections from the Swartberg Mountains are close to the typical form from the Outeniqua Mountains. A second Swartberg collection, *Thorne s.n.,* has longer bracts (14–20 mm long) and perianth tube (14–20 mm long), linking the unusual Thompson collection to those from the south.

Specimens examined. SOUTH AFRICA. CAPE: 3322 (Oudtshoorn) top of Swartberg Pass next to the road, 5,400 ft. (AC), *Vlok 812* (MO); summit of Spitzkop, W of Meirings Poort (AD), *Thorne s.n.* (SAM 50192); Swartberg, summit ridge SW of Blouberg, 5,800 ft., *Thompson 2226* (STE); Blesberg, near radio tower, 6,800 ft. (BC), *Vlok 805* (MO); Robinsons Pass, near water courses (CC), *Hops 17* (BOL); Cradock Peak, Montagu Pass (CD), *Zinn s.n.* (SAM 54824); Kleinberg Forest Reserve, Kammanassie Mts., 2,600 ft. (DA), *Mathews 1182* (NBG); Kammanassie Mts., Mannetjiesberg (DB), *Esterhuysen 4838* (BOL), *Bond 931* (NBG), *Mathews 1074* (NBG); S slopes of Mannetjiesberg, 4,000–5,000 ft., *Esterhuysen 18372* (BOL, K, PRE); Stormberg, Outeniqua Mts., steep S slopes (DD), *Taylor 1135* (SAM).

3323 (Willowmore) top of Prince Alfreds Pass, moist shady kloof (CC), *Lavranos 12676* (PRE); S slope, Formosa (DC), *Compton 4203* (BOL, NBG); Helpmekaar Peak, *Esterhuysen 4584* (BOL, PRE), *Bond 900* (NBG); Tsitsikamma Mts., S slopes near Joubertina, 3,500–4,000 ft. (DD), *Esterhuysen 18355* (BOL, PRE), *16852* (BOL); De Hoek, Uniondale, 3,500 ft., *Esterhuysen sub Fourcade 6533* (BOL).

3324 (Steytlerville) S slopes of Witte Els Berg, 2,000–2,400 ft. (CC), *Fourcade 2968* (BOL, K, MO, PRE, S, STE).

6. Geissorhiza foliosa Klatt, Linnaea 34: 658–659. 1866; Baker, Handb. Irid. 158. 1892, Fl. Cap. 6: 74. 1896; Foster, Contr. Gray Herb. 135: 62. 1941. TYPE: South Africa. Cape: Swellendam, "Berge bei Puspasvlei," *Ecklon & Zeyher Irid. 218* (70.10) [lectotype, B, effectively designated by Foster (1941); isolectotypes, B, BM, E, FI, K, L, LD, MO, P, PRE, S, SAM, W, Z].

Geissorhiza nigromontana Ecklon, Topogr. Verz. Pflanzensamml. Ecklon 21. 1827, nom. nud. et ms.
Geissorhiza eckloniana Pappe ms.

Plants 8–20(–30) cm high. *Corm* globose, asymmetric with an obliquely flattened side extending shortly downward, 5–10 mm diam., tunics concentric, dark brown, hard and woody, fragmenting irregularly into sections. *Cataphyll* pale, membranous, sometimes evidently lacking. *Leaves* 5 to several, erect to falcate, 3–6 mm wide, lanceolate to ensiform, typically short and seldom more than one-third as long as the stems, at least the lower 3–4 basal, the upper cauline and becoming smaller, sometimes 3–4 on a stem, uppermost often bract-like. *Stem* erect, simple or 1–2-branched, either from the base or from upper stem nodes. *Spike* 2–5-flowered; *bracts* 9–12(–15) mm long, evidently herbaceous, becoming membranous and dry above and often reddish along margins, inner usually slightly shorter than the outer. *Flowers* stellate, lilac to purple (colorless when faded), rarely white; *perianth tube* ca. 5 mm long, cylindric, included in the bracts; *tepals* 13–17 mm long, obovate, 6–7 mm wide. *Filaments* 4–5 mm long; *anthers* 4–6 mm long, pollen yellow. *Ovary* 2–3 mm long, *style* dividing at the apex of the anthers, branches 3–4 mm long, recurved. *Capsule* 7–9 mm long, narrowly ovoid. *Chromosome number,* unknown.

Flowering time. September to early November.

Distribution. Slopes and flats in the southern Cape at the foot of the Langeberg between Swellendam and Riversdale. Figure 23.

Geissorhiza foliosa is apparently related to the more common *G. inconspicua,* a predominantly montane species with a wider distribution, extending from the Langeberg near Swellendam to Port Elizabeth. It can always be distinguished from this species by its characteristic short, lanceolate leaves, which give it a very different appearance from other species of *Geissorhiza.* It differs from *G. inconspicua* also in its slightly larger flowers, with tepals 13–17 mm long and perianth tube, 5–6 mm long, which is always included in the bracts.

Geissorhiza nigromontana, a narrow endemic of the Great Swartberg Mountains, appears to be closely allied to *G. foliosa* and is perhaps a regional segregate of this species. Their similarities

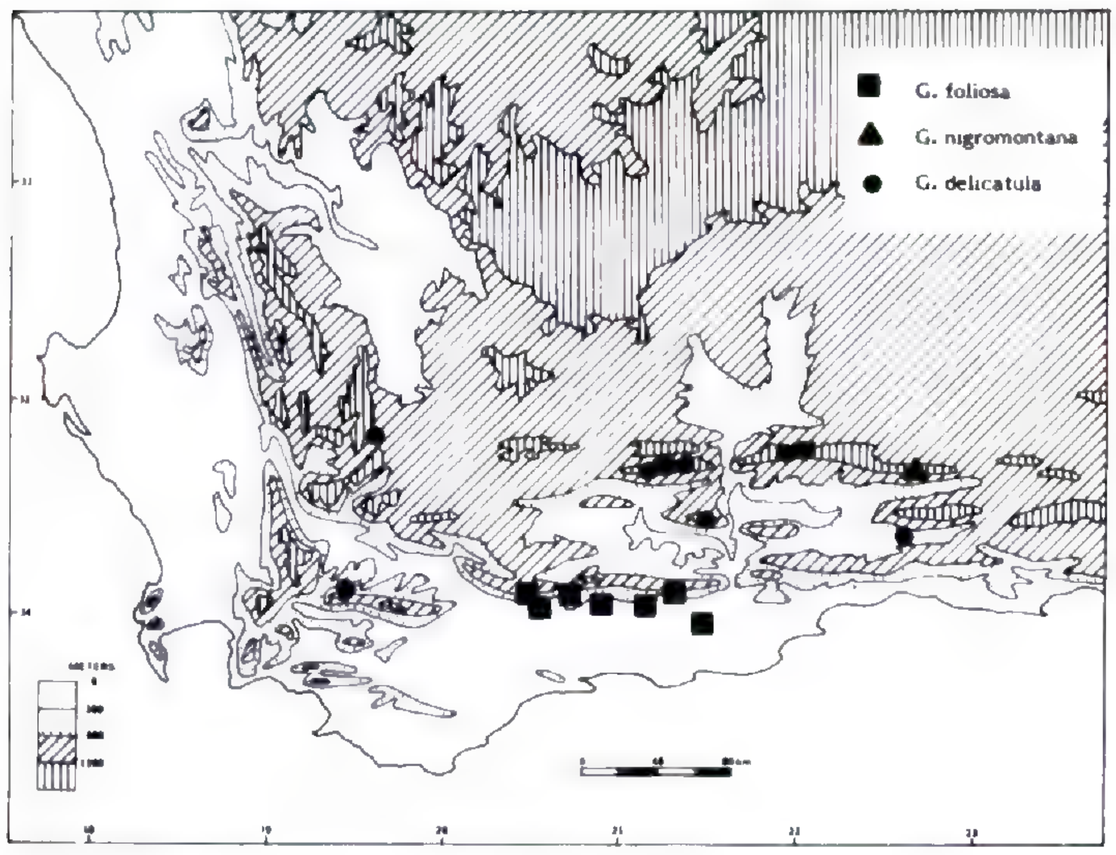


FIGURE 23. Distribution of *Geissorhiza foliosa, G. nigromontana,* and *G. delicatula.*

and differences are discussed under *G. nigromontana.*

Geissorhiza foliosa is poorly collected, and there are few recent collections of the species, despite the fact that it is recorded from a well-collected and easily accessible area.

Specimens examined. SOUTH AFRICA. CAPE: 3321 (Ladismith) Kampsheberg, 1,000 ft. (CD), *Muir 3336* (BOL).

3420 (Bredasdorp) Swellendam (AB), *Ross Frames s.n.* (BOL 31888); below 10 O'Clock Mt., Swellendam, in pastureland, *Wurts 438* (NBG), *480* (NBG); Koloniesbos, fynbos, *van Wyk 351* (STE); roadside near Zuurbraak (BA), *Hurling & Neil s.n.* (BOL 31889); Buffeljagsrivier bei Rietkuil, *Ecklon & Zeyher 3961* (124.10) (BM, BOL, FI, G, K, S, SAM, W, Z); Ruggens near Zuurbraak, 800 ft., *Galpin 4711* (BOL), *4715* (K, PRE); "Zwellendam, berge bei Puspas Valei, Duivelsbos etc." (BA-BB), *Ecklon & Zeyher Irid. 218* (70.10) (B, BM, E, FI, K, L, MO, P, PRE, S, SAM, W, Z); between Zuurbraak and Heidelberg (BB), *Lewis 5655* (NBG, STE).

3421 (Riversdale) near Riversdale (AA), *Muir 4718* (BOL); between Riversdale and Albertinia (AB-BA), *Stayner s.n.* (NBG 65206).

WITHOUT PRECISE LOCALITY: Caledon district, *Pappe s.n.* (SAM 20879).

7. Geissorhiza nigromontana Goldbl., sp. nov. TYPE: South Africa. Cape: Groot Swartberg, Blesberg at Tierkloof, along stream, *Vlok 93* (holotype, MO; isotypes, NBG, SAAS).

Planta 10–16 cm alta, tunicis cormi manifeste concentricis, papyraceis, foliis 3–6 inferioribus duobus basalibus, 4–10 mm latis falcatis, caule infra manifeste prostrato supra erecto, infra bulbilifero, spica 2–3 florum, floribus verosimiliter stellatis, caeruleo-purpureis, tubo ca. 2 mm longo, tepalis 14–16 mm longis, antheris ca. 5 mm longis, stylo diviso ad medium antherarum, ramis recurvatis.

Plants 10–16 cm high. *Corm* globose, asymmetric with an obliquely flattened side extending downward shortly, ca. 6 mm diam., tunics apparently concentric, light brown, outer layers apparently brittle-papery. *Cataphyll* pale, membranous. *Leaves* 3–6, falcate, at least the lower two basal, upper cauline and becoming smaller, sometimes 3–4 on a stem, the uppermost often bract-like, 4–10 mm wide, reaching to the base of the spike or only half to one-third as long as the stem. *Stem* apparently prostrate below, erect above, simple or sometimes branched, both from the base or from upper stem nodes, bearing cormlets from the lower nodes. *Spike* 2–3-flowered; *bracts* 8–10 mm long, green, becoming membranous above, the inner slightly shorter than the outer. *Flowers* apparently stellate, blue-purple; *perianth tube* 2–3 mm long, cylindric, included in the bracts; *tepals* 14–16 mm long, obovate, ca. 6 mm wide. *Filaments* ca. 6 mm long; *anthers* about 5 mm long, pollen yellow. *Ovary* ca. 3 mm long; *style* dividing at about the midline of the anthers, branches long, 4–5 mm long, recurved. *Capsule* unknown. *Chromosome number,* unknown.

Flowering time. January to February.

Distribution. Great Swartberg Mountains, local along streams on Blesberg at ca. 1,800 m. Figure 23.

Geissorhiza nigromontana is apparently a narrow endemic of the Swartberg Mountains, where it has been collected only twice by J. J. Vlok in 1981 and 1985. It blooms towards the end of summer, in January and probably into February, in this area of low rainfall and depends for moisture on the permanent streams along which it grows.

It apparently has fairly soft corm tunics, but few of the specimens available have corms, and their exact nature is difficult to assess with so little material to examine. *Geissorhiza nigromontana* is most probably closely related to *G. foliosa,* a species of the Langeberg foothills, which blooms mainly in the months of October and November, and it has the broad flat leaves typical of that species. It is distinctive in its short tubed flower, with the tube ca. 2 mm long, few flowered spike and relatively long style branches 4–5 mm long. In contrast, *G. foliosa* has a tube 5–6 mm long, a spike of (1–)3–7 but usually several flowers and style branches to 3 mm long. *Geissorhiza nigromontana* is also distinctive in bearing cormlets in the lower stem axils, a characteristic rare in the genus.

Specimens examined. SOUTH AFRICA. CAPE: 3322 (Oudtshoorn) lower S slopes of the Swartberg next to waterfall, near Rus en Vrede (AD), *Vlok 893* (MO, NBG, SAAS); Groot Swartberg, Blesberg at Tierkloof, along stream (BC), *Vlok 93* (MO, NBG, SAAS).

8. Geissorhiza delicatula Goldbl., sp. nov. TYPE: South Africa. Cape: shady mountainside, Seven Weeks Poort, *Compton 4016* (holotype, NBG; isotype, BOL).

Planta 3–9(–12) cm alta, foliis 3–6, inferioribus 2–4 basalibus planis, superiore caulem vaginanti, caule erecto simplici vel ramoso, bracteam brevem ferenti, ramis unifloribus raro ad 4 florum, floribus stellatis, pallide caeruleis, tubo 2–3 mm longo, tepalis 7–12 mm longis, antheris 2.5–3.5 mm longis, stylo diviso prope apicem antherarum, ramis recurvatis.

Plants 3–9(–12) cm high. *Corm* globose, asymmetric with an obliquely flattened side extending downward shortly, 3–8 mm diam., tunics concentric, brown, firm to soft membranous, fragmenting irregularly into sections. *Cataphyll* brown to transparent, membranous, sometimes conspicuous. *Leaves* 3–6, erect to falcate, 1.5–4.5 mm wide, linear to ensiform, often prostrate, half as long as the stems, at least the lower 2–3 basal, the upper cauline and becoming smaller, uppermost often bract-like. *Stem* erect, simple or 1–3-branched, either from the base or from the upper nodes. *Spike* usually 1, rarely to 3-flowered; *bracts* 4–8 mm long, herbaceous, becoming membranous and dry above and sometimes reddish along the margins, the inner about as long as the outer. *Flowers* stellate, pale lilac purple, cream in the throat and tube; *perianth tube* 2–3 mm long, cylindric, included in the bracts; *tepals* 7–12 mm long, obovate, 2.5–4.5 mm wide. *Filaments* 3–5 mm long; *anthers* 2.5–3.5 mm long, pollen yellow. *Ovary* 1.5–3 mm long, *style* dividing towards the apex of the anthers, branches to 1.5 mm long, recurved. *Capsule* 4–7 mm long, narrowly obovoid. *Chromosome number,* unknown.

Flowering time. August to September in drier sites, November to December at higher altitudes.

Distribution. Sheltered places in the interior mountains of the western and southern Cape from Jonas Kop in the west to the Swartberg Pass in the east. Figure 23.

Geissorhiza delicatula is apparently related to the more well known *G. inconspicua* and *G. foliosa,* both predominantly montane species of the wetter coastal ranges, extending from the Langeberg at Swellendam to near Port Elizabeth. It is always a much smaller and more delicate plant and it can be distinguished from these species by its normally single branched stems. Even the most robust individuals of *G. delicatula* seem to have this habit. It also differs from *G. inconspicua* and *G. foliosa* in its slightly smaller flowers, with tepals 7–12 mm long and short perianth tube, 3–4 mm long, which is always included in the bracts. *Geissorhiza inconspicua* and *G. foliosa* normally have flowers with tepals 8–17 mm long and a tube 4–6 mm long, and typically have spikes of 3–6 flowers.

A collection from the Swartberg, *Oliver 3056,* seems to differ in having leaves of a somewhat firmer texture than other collections. It also has larger flowers than most other gatherings of the species, but at least in the flower size, a collection from nearby, *Stokoe s.n.* from the Swartberg Pass, is comparable. From the material available, it seems best to regard these specimens merely as a form of *G. delicatula.* All the collections of the species except *Oliver 5359* from the Rooiberg, have single flowered branches. The Oliver gathering, however, includes plants with one, two, or three flowers per branch. It is possible that this collection represents a very depauperate form of *G. inconspicua.*

Specimens examined. SOUTH AFRICA. CAPE: 3319 (Worcester) Karoopoort (BA), *Hafstrom & Acocks 288* (PRE, S); Jonas Kop, ca. 3,000 ft., wet shaded sites on S side of overlying rocks (DC), *Goldblatt 4723* (MO), *5880* (MO).

3321 (Ladismith) Buffelskloof, Swartberg near Ladismith (AC), *Esterhuysen 14007* (BOL); shade on S slopes below Towerkop, *Esterhuysen 13967* (BOL); Seven Weeks Poort, mountain slopes, SW aspect (AD), *Esterhuysen 24838* (BOL); shady mountainside, Seven Weeks Poort, *Compton 4016* (BOL, NBG); above Seven Weeks Poort, *Phillips 1543* (SAM); Swartberg, between Waboomsberg and Kangoberg, 6,000 ft. (BD), *Oliver 3056* (PRE, STE); Rooiberg, summit ridge above Assegaaiboskloof (DA), *Oliver 5379* (STE).

3322 (Oudtshoorn) 8 mi. W of the top of Swartberg Pass (AC), *Stokoe s.n.* (SAM 68346); Langkloof, road to Daskop near turnoff to Matjesrivier (DC-DD), *Vlok 301* (MO).

9. Geissorhiza bracteata Klatt, Abh. Naturf. Ges. Halle 15: 391 (Erg. 57) 1882; Baker, Handb. Irid. 158. 1892, Fl. Cap. 6: 74. 1896; Foster, Contr. Gray Herb. 135: 62. 1941. TYPE: South Africa. Cape: Olifantshoek, Uitenhage, *Ecklon & Zeyher s.n.* (holotype, B "Herb. Lubeck"), *Ecklon & Zeyher Irid. 221* (10.9) (B, BM, E, FI, G, LD, MO, PRE, S, W, Z, from the same locality are probably isotypes). FIGURE 24.

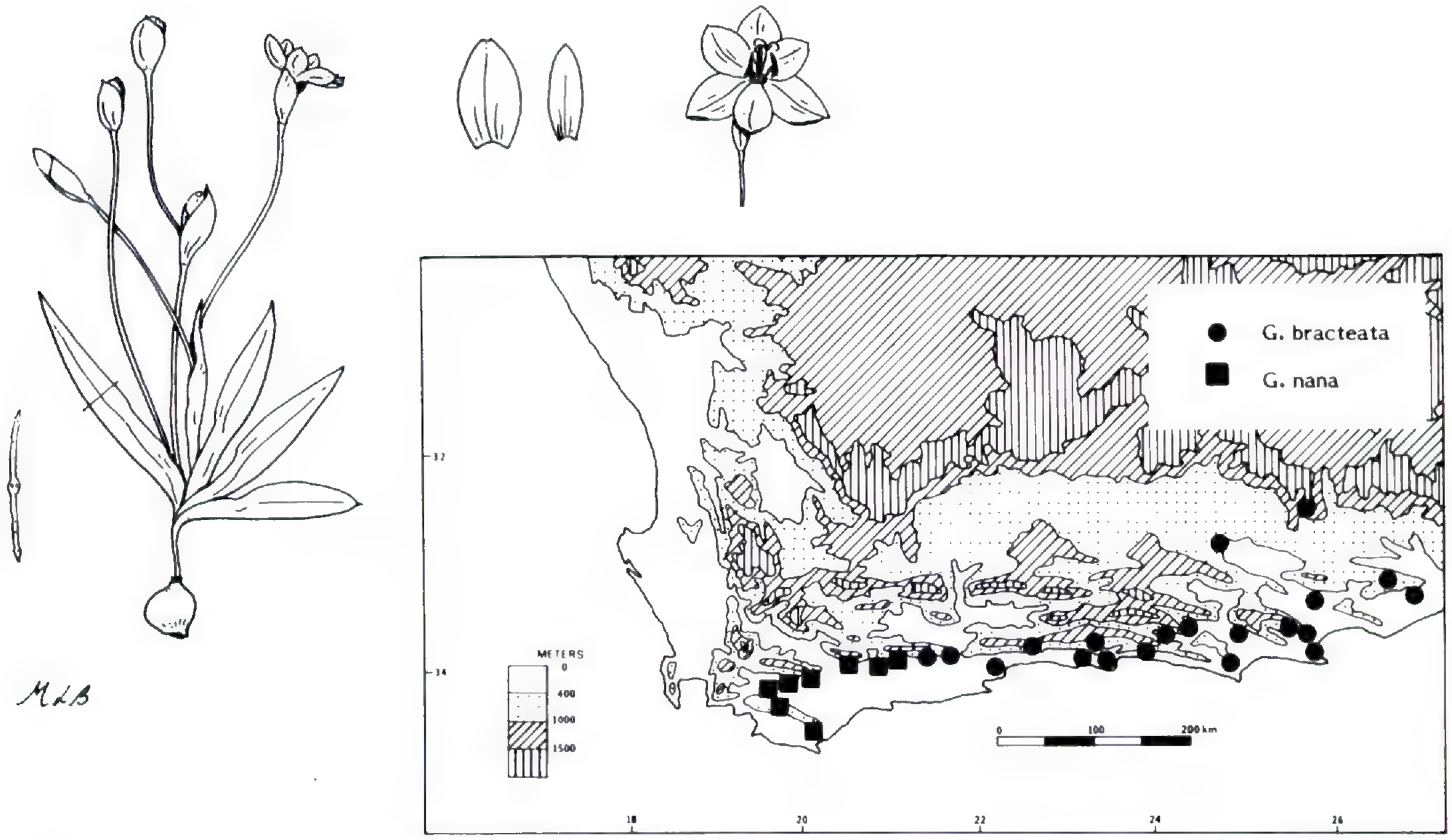


FIGURE 24. Morphology of *Geissorhiza bracteata* and distribution of *G. bracteata* and *G. nana*. Habit ×0.5; flower and separated outer and inner bracts life size; leaf section much enlarged (no voucher, Uitenhage).

Weihea elatior Ecklon, Topogr. Verz. Pflanzensamml. Ecklon 22. 1827, nom. nud.
Geissorhiza tabularis var. *elatior* Ecklon ms. [*Ecklon & Zeyher Irid. 221* (10.9)].
Geissorhiza recurvifolia (Poir.) Klatt sensu Klatt, Linnaea 34: 655. 1866, pro parte excl. basion.

Plants (4–)6–18 cm high. *Corm* ovoid, asymmetric with an oblique flat side extending shortly downward, 4–6 mm diam., tunics pale to dark brown, concentric, the outer layers fragmenting irregularly into sections and drawn into points above. *Cataphyll* pale, membranous. *Leaves* (3–)4 to several, the lower basal, upper cauline and becoming smaller, sometimes bract-like, 2–9 mm wide, ensiform, half to one-third as long as the stems. *Stems* erect, single or 2–5 produced from base and occasionally higher on the stem. *Spike* usually 1-flowered, rarely 2–3; *bracts* green, often reddish along the margins, 6–10 mm long, the inner usually slightly shorter than the outer. *Flowers* stellate, white, the outer tepals sometimes red-flushed on the reverse; *perianth tube* 3–5 mm long, infundibuliform, widening from the base; *tepals* (5–)8–12 mm long, obovate, 4.5–6 mm wide. *Filaments* 5–7 mm long; *anthers* 2–3.5 mm long, pollen yellow. *Ovary* 2–3 mm long; *style* dividing at the apex of the anthers, branches recurved. *Capsule* 7–9 mm long, narrowly ovoid, seeds angular. *Chromosome number*, $2n$ = ca. 52 (*Goldblatt 4933*).

Flowering time. September to mid-October.

Distribution. Southern and eastern Cape, from Albertinia east to Grahamstown and in the southern Karoo, often in clearings or on edge of forest. Figure 24.

Geissorhiza bracteata is one of the least specialized species in the genus, having several flat, ensiform leaves, a branched stem, and concentric corm tunics, all of which are considered primitive in *Geissorhiza*. It is closely allied to *G. inconspicua* and sometimes difficult to separate from that species. It can be recognized by its 1(–3)-flowered spikes and branches produced from the base of the plant. *Geissorhiza inconspicua* is a variable species, and depauperate, few flowered specimens of the white-flowered form approach *G. bracteata*. It is also possible to confuse *G. bracteata* (e.g., *Bayliss 6035, Duthie 1132*) with *G. setacea* although *G. setacea* generally has much shorter and narrower leaves, typically less than 2 mm wide. *Geissorhiza setacea* occurs on damp sandy flats in the southwestern Cape. This is well to the west of the range of *G. bracteata*, which is centered in the eastern Cape between Grahamstown and Humansdorp, although populations have been recorded as far to the west as Albertinia.

Geissorhiza bracteata appears to be a polyploid species, $2n$ = ca. 52, at least on the basis

of counts for one population. This population, from near Hankey, has proved in the greenhouse to be autogamous, which is unusual in *Geissorhiza*.

Specimens examined. SOUTH AFRICA. CAPE: 3224 (Graaf Reinet) near Jansenville (DC), *Bayliss 5925* (BR, K, MO, WAG).

3225 (Somerset East) Cradock Common (BA), *Bayliss 4967* (GH, MO, UC, US).

3321 (Ladismith) Welgevonden near Plattebosch, Albertinia (DC), *Muir 1811* (BOL); Cloetes Pass (DD), *Goldblatt 4158* (MO).

3322 (Oudtshoorn) Cradock Berg, George (CD), *Galpin 4673* (K, PRE); George, *Lewis 5603* (NBG).

3323 (Willowmore) Avontuur-George road, farm Arbor Nook, Pootjiesrivierhoogte (CA), *Snijman 365* (NBG); station above Uplands, 11.3 mi. from Kruis River Nek (CC-CD), *Fourcade 6112* (STE); Lottering (DC), *Fourcade s.n.* (BOL).

3324 (Steytlerville) Kromme River, 4 mi. W of Company's Drift (CC), *Fourcade 2317* (BOL); Bo Plaas, near Humansdorp (CD), *Bayliss 6035* (MO); 5.5 km N of Hankey (DD), *Goldblatt 4933* (K, MO, PRE, US).

3325 (Port Elizabeth) hills at Addo (BC-DB), *Ecklon & Zeyher Irid. 220* (SAM), *Ecklon & Zeyher Irid. 221* (S); Zuurberg Pass, cool SE-facing slopes (BD), *Snijman 489* (MO, NBG); Groendal Wilderness Reserve (CA), *Scharf 1493* (PRE); Despatch, Uitenhage (CD), *Holland 2209* (BOL), *Holland s.n.* (Nat. Bot. Gard. 2687/25 in BOL); Port Elizabeth (DC), *Fries, Norlindh & Weimarck 216* (LD, SAM), *Paterson 152* (BOL).

3326 (Grahamstown) Grahamstown (BC), *MacOwan 339* (SAM); along the the rivulet at Grahamstown, *Burchell 3546* (K); Mountain Drive, Grahamstown, *Bayliss 7231* (MO); Brickfields, Grahamstown, *Daly 861* (B, BOL, Z); Hopewell, S of Southwell (BD), *Acocks 16127* (PRE).

3422 (Mossel Bay) between Malgaten and Great Brak Rivers (AA), *Fourcade 6481* (BOL); turf near Church, Belvedere, Knysna (BB), *Duthie 1132* (BOL, MO, STE).

3423 (Knysna) flats 14 mi. E of Knysna (AA), *Gillett 1348* (BOL).

3424 (Humansdorp) hillside, Humansdorp (BB), *Galpin 4674* (K, PRE).

WITHOUT PRECISE LOCALITY: Riversdale hills, *Schlechter s.n.* (B); Uitenhage, *Ecklon & Zeyher s.n.* (10.9) (B, L); Zuurberg near Uitenhage, *Loubser 898* (NBG); Cape, *Krebs 799* (B), *Verreaux s.n.* (G); Olifantshoek, Uitenhage, *Ecklon & Zeyher Irid. 221* (10.9) (B, BM, E, FI, G, LD, MO, PRE, W, Z); Uitenhage, *Zeyher s.n.* (K); Mossel Bay-Barrington, *Fries, Norlindh & Weimarck 1287* (K, LD, PRE).

10. Geissorhiza nana Klatt, Abh. Naturf. Ges. Halle 15: 391 (Erg. 57). 1882; Baker, Handb. Irid. 157. 1892, Fl. Cap. 6: 73. 1896; Foster, Contr. Gray Herb. 135: 60–61. 1941. TYPE: South Africa. Cape: "Rivierzondereinde," Swellendam, *Ecklon & Zeyher 3967* (90.9) (as *Drège 3969*) (holotype, B "Herb. Lubeck"; isotypes, B, FI, G, K, S, SAM, W, Z).

Plants tiny, 2.5–4(–8) cm high. *Corm* narrowly ovoid, asymmetric, with an oblique flat side, 3–5 mm diam., tunics pale, concentric, drawn into bristles above. *Cataphyll* pale, membranous. *Leaves* (3–)4–6, usually all basal, or uppermost inserted on the lower part of the stem, flat, half as long, to slightly longer than the stem, 1–2 mm wide, linear-ensiform. *Stems* erect, single, or to 4, produced from near the base, rarely branched above. *Spike* 1–2(–3)-flowered; *bracts* 4–6 mm long, green, sometimes red along the margins. *Flowers* tiny, stellate, white, red-brown on the reverse of the outer tepals; *perianth tube* 1–2.5 mm long, nearly cylindric; *tepals* obovate, 3–6 (–8) mm long. *Filaments* ca. 2 mm long; *anthers* 1.2–1.8 mm long. *Ovary* ca. 2 mm long; *style* dividing at mid-anther level, branches less than 1 mm long, recurved. *Capsule* 4–6 mm long, obovoid, usually slightly exceeding bracts. *Chromosome number,* $2n = 26$ (*Goldblatt s.n.* no voucher, near Swellendam).

Flowering time. September to early October.

Distribution. Clay flats and slopes in renosterbosveld, in the Caledon district and eastwards to Heidelberg. Figure 24.

Geissorhiza nana is a very dwarf species of *Geissorhiza* clearly related to the southern and eastern Cape *G. bracteata*. It is in fact difficult to distinguish depauperate forms of the latter from *G. nana*. The flower is critical in separating the two: *G. nana* has tiny flowers with tepals 3–6 mm long, with very pronounced darker markings on the reverse of the outer tepals, while *G. bracteata* usually has quite large flowers with tepals in the 8–12 mm long range, and coloring on the reverse of the outer tepals is rare. Difficulties are, however, experienced in distinguishing *G. nana* from the depauperate forms of *G. bracteata* found in the southern Cape, which may have tepals as short as 6–7 mm, but even these plants are usually larger than *G. nana*.

There is also the possibility of confusing *Geissorhiza nana* with *G. setacea,* another dwarf species of section *Weihea*. *Geissorhiza setacea* is very similar in general appearance, but it is larger in all features, having flowers with a tube ca. 6 mm long and tepals in the 8–12 mm range. *Geissorhiza setacea* grows on damp sandy flats along the western Cape coastal belt, whereas *G. nana* grows in drier clay soils in the southern Cape.

My impression is that *Geissorhiza nana* is not uncommon in renosterbosveld from the Caledon district east to Riversdale. The few collections

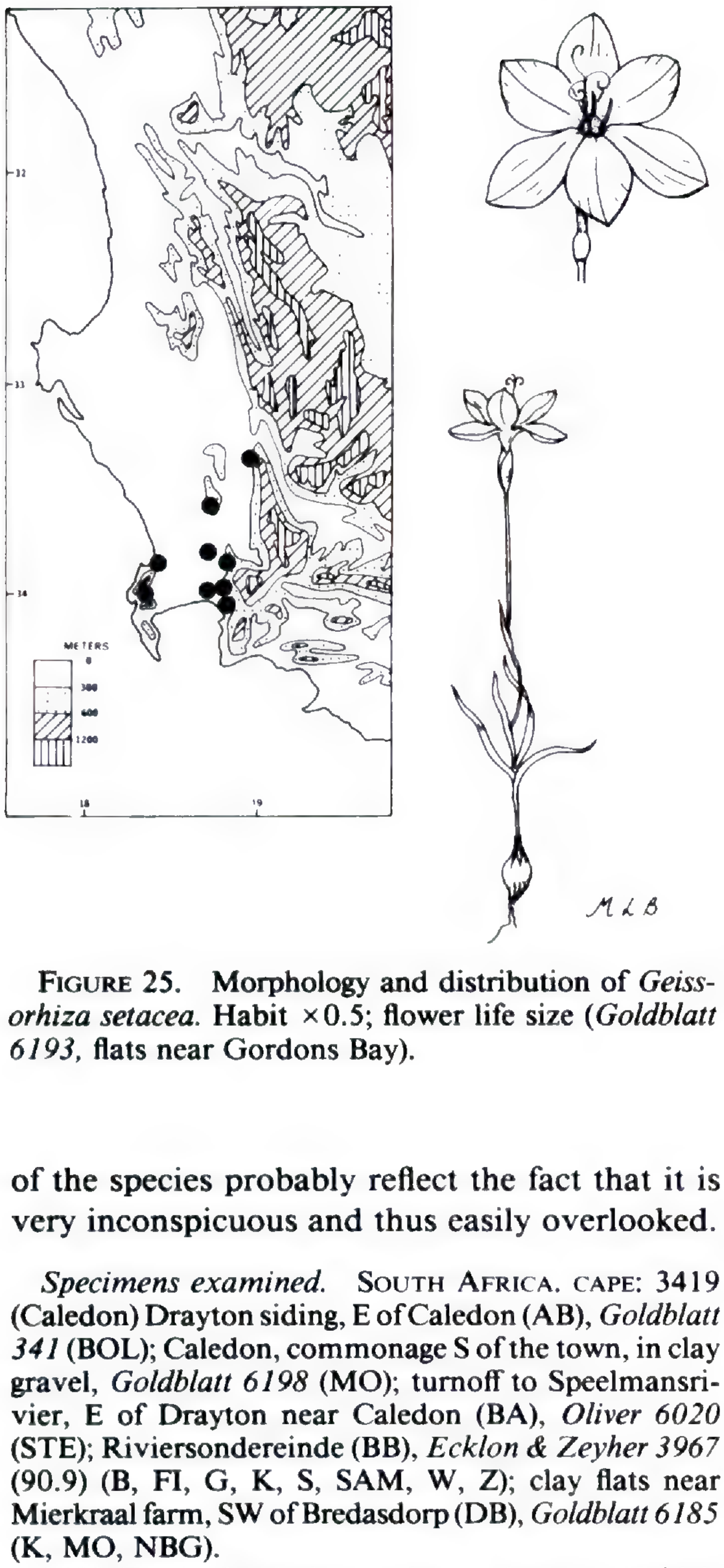


FIGURE 25. Morphology and distribution of *Geissorhiza setacea*. Habit ×0.5; flower life size (*Goldblatt 6193*, flats near Gordons Bay).

of the species probably reflect the fact that it is very inconspicuous and thus easily overlooked.

Specimens examined. SOUTH AFRICA. CAPE: 3419 (Caledon) Drayton siding, E of Caledon (AB), *Goldblatt 341* (BOL); Caledon, commonage S of the town, in clay gravel, *Goldblatt 6198* (MO); turnoff to Speelmansrivier, E of Drayton near Caledon (BA), *Oliver 6020* (STE); Riviersondereinde (BB), *Ecklon & Zeyher 3967* (90.9) (B, FI, G, K, S, SAM, W, Z); clay flats near Mierkraal farm, SW of Bredasdorp (DB), *Goldblatt 6185* (K, MO, NBG).

3420 (Bredasdorp) clay road verge between Heidelberg and Strawberry Hill (BB), *Goldblatt 4961* (MO); Palmyra, Heidelberg, *Loubser 2126* (NBG).

3421 (Riversdale) Korente River Dam, clay hill (AA), *Bohnen 6663* (STE).

11. Geissorhiza setacea (Thunb.) Ker, Ann. Bot. (König & Sims) 1: 224. 1804, Bot. Mag. tab. 1255. 1810 (misapplied to *G. hispidula* Goldbl.); Baker, Fl. Cap. 6: 74. 1896, pro parte; Foster, Contr. Gray Herb. 135: 64. 1941. *Ixia setacea* Thunb., Diss. de *Ixia* no. 13: 146. 1783. TYPE: South Africa. Cape: without precise locality, *Thunberg s.n.* [lectotype, Herb. Thunb. 995, effectively designated by Foster (1941); isolectotypes, S "Herb. Osbeck," "Herb. Alstroemer," "Herb. Montin"]. FIGURE 25.

Plants small, 4–8 cm high. *Corm* globose, asymmetric, one side flattened below and extending downward in a fan-like ridge, 3–4 mm diam., tunics concentric, outer layers irregularly fragmented. *Cataphyll* membranous. *Leaves* usually 4, the lower three basal, about half as long as stem, erect to falcate, linear-ensiform, 1–2.5 mm wide, lamina flat, the uppermost leaf cauline, usually smaller than the basal leaves, the lower half sheathing the stem. *Stem* erect, occasionally 1 or rarely 2-branched. *Spike* 1(–rarely 2)-flowered; *bracts* 5–7 mm long, herbaceous, the upper margin sometimes reddish, the inner slightly longer than the outer. *Flower* hypocrateriform, cream white or pale yellow with a dark center, flushed red to purple on the reverse of the outer tepals especially with age; *perianth tube* ca. 6 mm long, infundibuliform; *tepals* (8–)10–12 mm long, obovate, 6–8 mm wide. *Filaments* 3–4 mm long; *anthers* 2.5–4 mm long. *Ovary* ca. 3 mm long; *style* dividing at the apex of the anthers, branches recurved. *Capsule* unknown. *Chromosome number,* unknown.

Flowering time. July to August (to September).

Distribution. Wet flats in the southwestern Cape from the Peninsula east to the foot of the Hottentots Holland Mountains and north to Gouda. Figure 25.

This small species can easily be recognized by its fairly large, and relatively long-tubed flowers borne singly on short stems. Its corm tunics are of the concentric type, and it belongs in subgenus *Weihea,* near *Geissorhiza bracteata* and *G. nana. Geissorhiza setacea* can readily be distinguished from these species by its large flower, with tepals 8–12 mm long, on a very small plant seldom exceeding 8 cm in height. The very dwarf *G. nana* is similar but smaller, usually only 4–5 cm high and has tiny flowers with tepals 3–6 mm long. It is typical of clay soils in contrast to *G. setacea* which grows on damp and often waterlogged sandy flats.

It was one of the early species of *Geissorhiza* to be named, having been described by Thunberg in 1783, as *Ixia setacea,* from material he collected during his travels at the Cape in the years 1772–1775. It has generally been recognized as a distinct species of *Geissorhiza,* although partly confused with *G. bracteata* by J. G. Baker (1896)

and Foster (1941), both of whom included specimens of *G. bracteata* under *G. setacea.* This confusion is understandable as depauperate forms of *G. bracteata* do resemble *G. setacea.* The plant illustrated by Ker (1810) as *G. setacea* in the Botanical Magazine tab. 1255 is *G. hispidula* Goldbl. (*G. humilis* var. *bicolor* Baker), a different and not very closely related species.

Geissorhiza setacea usually has white flowers, but in the north of its range, near Gouda, at Elandsberg farm there is a creamy yellow form, which has a blackish center. This form grows sympatrically with and blooms at the same time as *G. purpureolutea* which has almost identical flowers, but imbricate corm tunics and ribbed leaves and belongs in subgenus *Geissorhiza.* This is one of several examples of floral convergence found in *Geissorhiza,* where similar flower color and marking occur repeatedly in unrelated species or in other genera.

Specimens examined. SOUTH AFRICA. CAPE: 3318 (Cape Town) near Cape Town (CD) *H. Bolus 4804* (BOL), *4803* (E, K, Z); Table Mt. near Orange Kloof, *Schlechter 412* (Z); flats near Hoorn Kloof, Paardeberg, *Lewis & Salter 3556* (BM, BOL, K); near Stellenbosch (DD), *Duthie 521* (BOL); Stellenbosch, Golf Course, *Strey 551* (PRE); Stellenbosch flats, *Garside 279* (K), *Bos 323* (PRE, WAG); outside Duthie Reserve, Stellenbosch, *Bos 328* (STE); clay slope 300 ft. N of Bottelary Road, *Acocks 2452* (S).

3319 (Worcester) Elandsberg farm, S of Gouda, wet flats (AC), *Goldblatt 6210* (K, MO, NBG, PRE, S).

3418 (Simonstown) Van Der Stel, Stellenbosch (BB), *Smith 3204* (PRE); low lying, wet area SW of Somerset West, *Boucher & Mauve 4946* (PRE); sandy flats between Strand and Gordon's Bay, *Parker 4227* (BOL, K, NBG), *Goldblatt 6193* (K, MO, NBG); Faure, flats waterlogged in winter, *Parker 3972* (BOL, K, NBG); Sir Lowrys Pass, *Stokoe s.n.* (SAM 49615), *Schlechter 1154* (B, BM, G, Z).

WITHOUT PRECISE LOCALITY: Caledon, *Pappe s.n.* (SAM 55323); Cape, *Thunberg s.n.* (Herb. Thunb. 995 UPS, S), *Oldenberg 489* (BM).

12. Geissorhiza ornithogaloides Klatt, Linnaea 34: 656. 1866. TYPE: South Africa. Cape: Caledon Zwartberg and about the Baths, *Ecklon & Zeyher Irid. 225* (51.8) (lectotype, B, here designated; isolectotypes, B, BM, BOL, E, FI, G, GH, L, LD, MO, W, Z); Worcester, Tulbaghskloof, Winterhoeksberg, Tulbaghsthal etc., *Ecklon & Zeyher Irid. 224* (77.9) (syntypes, B, LD, MO, S); Koue Bokkeveld, *Lichtenstein 15* (syntype, B) [chosen arbitrarily by Foster as lectotype for *G. ornithogaloides,* being the first of the three cited type collections; it lacks a corm and cannot be certainly identified and distinguished from *G. ornithogaloides* subsp. *marlothii* (syn. *G. marlothii*)]. FIGURE 26.

Plants small, 4–10 cm high. *Corm* either more or less ovoid or campanulate in outline with a broad flat base, 4–6 mm at widest diam., tunics medium brown, concentric, either fragmenting into elliptical sections or, in two parts, a campanulate cap and basal plate, then lower margins of cap toothed. *Cataphyll* membranous, often evidently lacking. *Leaves* usually 4, the lower two basal, linear to lanceolate, erect to falcate, 1–2 (–3) mm wide, flat, the upper two inserted on the stem at or above ground level, and sheathing below, the sheath often inflated. *Stem* erect, usually branching from both cauline leaves. *Spike* 1(–rarely 2)-flowered; *bracts* pale green, becoming dry above, 7–10 mm long. *Flower* clear yellow, stellate; *perianth tube* 2–3 mm long, not exserted from the bracts; *tepals* obovate (6–)7–12(–18) mm long, 3.5–6 mm wide. *Filaments* 2–4 mm long, erect; *anthers* 3–4.5 mm long, yellow. *Ovary* ca. 2 mm long, *style* dividing at the apex of the anthers, branches 2–3 mm long and recurved. *Capsule* obovate, 7–9 mm long, usually exceeding bracts. *Chromosome number,* $2n = 26$ (*Goldblatt 214* as *G. nana*).

Flowering time. Late August to October.

Distribution. Sandy and clay flats and slopes from the Paarl district eastward through the Cold Bokkeveld, Worcester district and southern Cape to the Long Kloof. Figure 26.

Geissorhiza ornithogaloides is typically a dwarf and rather slender species with unusual, bright yellow flowers. It is morphologically variable and some plants in a population may be robust and much larger flowered than others, e.g., *Lewis 6052,* and the extremes almost seem different species. The vegetative morphology is however, remarkably uniform, with plants always having spikes with either one or two flowers, two narrow, flat, basal leaves, and two cauline and partly sheathing leaves.

This pattern is found in *Geissorhiza marlothii,* a species which is identical to *G. ornithogaloides* in all features except the corm, the reason that Foster (1941) recognized the former as distinct. *Geissorhiza marlothii* has a small corm with concentric tunics of the type characteristic of all species of subgenus *Weihea.* The corm of *G. ornithogaloides* is unusual in the genus, being campanulate in outline, with an oblique flat base and

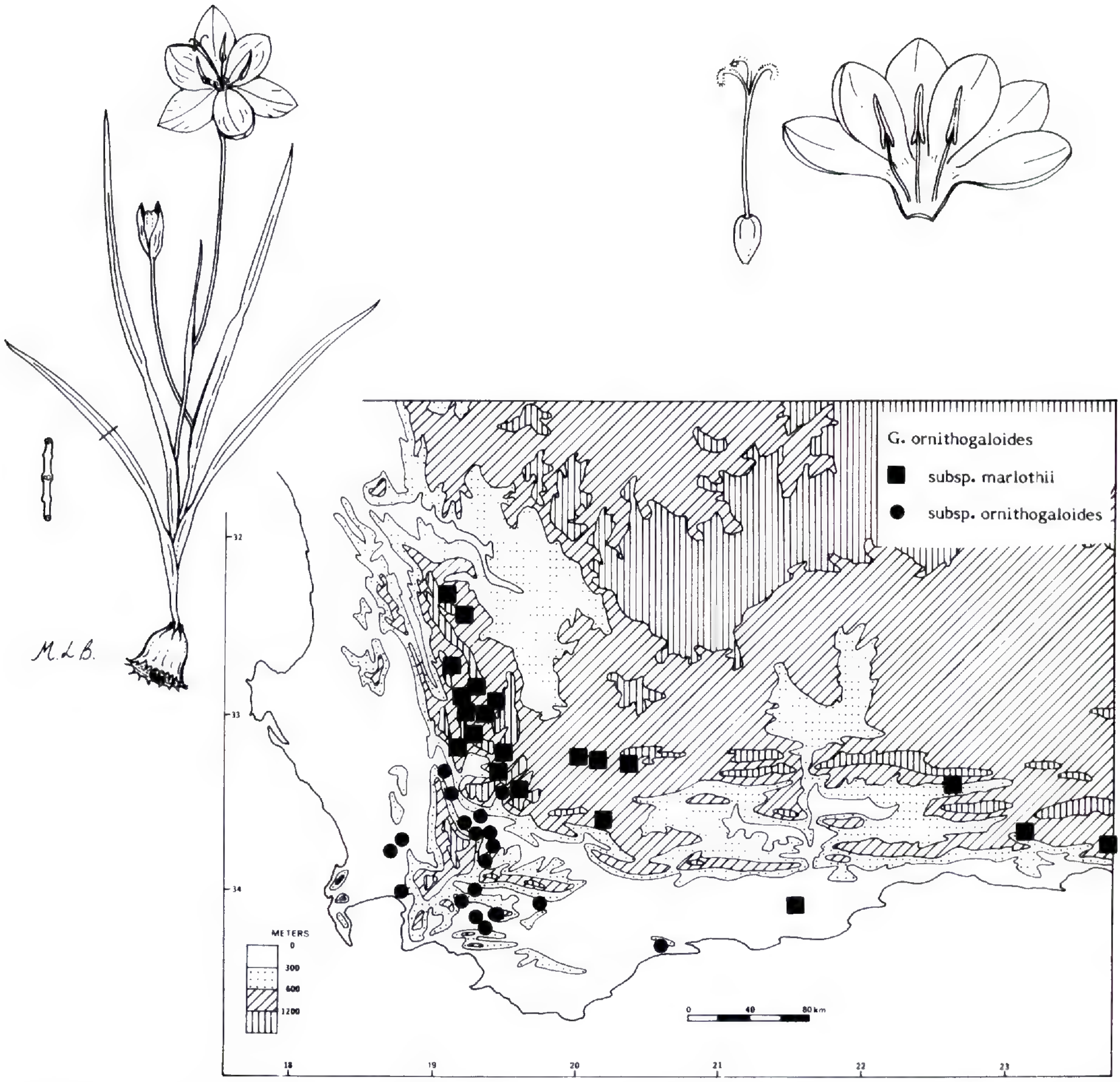


FIGURE 26. Morphology and distribution of *Geissorhiza ornithogaloides*. Habit with flower life size; opened flower and gynoecium ×2 (*Goldblatt 6202,* Villiersdorp-Brandvlei).

serrate lower margins. The morphological similarity between the two species, excepting the corms, seems to me so striking, however, that I prefer to treat *G. marlothii* as a subspecies of *G. ornithogaloides*.

The only close ally of *Geissorhiza ornithogaloides* is *G. malmesburiensis*, described by Foster in 1941 on the basis of a single Schlechter collection, which lacked corms. A second sheet of the Schlechter collection, and collections made by Lewis and by myself, have corms which are exactly like those of the typical subspecies of *G. ornithogaloides*, which substantiates Foster's belief that they were in fact closely related. *Geissorhiza malmesburiensis*, in fact, differs from all forms of *G. ornithogaloides*, mainly in its large flower size which contrasts with its very dwarf vegetative morphology.

I have found it necessary to alter the lectotypification of *Geissorhiza ornithogaloides*, the reasons being as follows. Of the three collections cited by Klatt in the protologue, two are Ecklon and Zeyher collections from the Caledon district, both widely well-distributed in major herbaria, and often complete with corms. The first specimen cited, however, is a Lichtenstein collection supposedly from the Cold Bokkeveld which today lacks corms, though they were present at one time according to the description. Both the distribution and description of the corms suggests

that this last collection is *G. marlothii,* yet was chosen as lectotype by Foster, for *G. ornithogaloides,* a species only distinguishable from *G. marlothii* by its corms. Foster was clearly arbitrary in choosing this first cited collection as lectotype, and I propose in place *Ecklon & Zeyher Irid. 225* in the Berlin Herbarium as the lectotype. The present interpretation of *G. ornithogaloides* is in this way preserved.

The two subspecies of *Geissorhiza ornithogaloides* are treated below, with subsp. *marlothii* first, as it is clearly the less specialized, having corms of the basic type for the subgenus, whereas corms of subsp. *ornithogaloides* are unusual and must be regarded as derived.

KEY TO THE SUBSPECIES OF *GEISSORHIZA ORNITHOGALOIDES*

1a. Corm nearly ovate, tapering at both ends, not campanulate in outline; and lower margins of tunics not or rarely slightly serrate ..... subsp. *marlothii*

1b. Corm campanulate with an oblique flat base; the lower margins of the tunics serrate ..... subsp. *ornithogaloides*

12A. Subsp. **marlothii** (Foster) Goldbl., comb. et stat. nov., *Geissorhiza marlothii* Foster, Contr. Gray Herb. 135: 66. 1941. TYPE: South Africa. Cape: Cold Bokkeveld, Houdenbeck, 850 m, *Marloth 10612* [holotype, B; isotypes, PRE, STE (without corms)].

? *Ixia ornithogaloides* Licht. ex Roem. & Schult., Syst. Veg. 1: 376. 1817. TYPE: South Africa. Cape: Koue Bokkeveld, *Lichtenstein 15* (holotype, B). (Specimens lack corms needed to distinguish the species from *G. ornithogaloides* Klatt, but from the stated locality, must be subsp. *marlothii.* This is not the basionym of *G. ornithogaloides* Klatt.)

Corm nearly ovoid, tapering at both ends, obliquely flattened below on one side, sometimes with the flat part extending downward conspicuously, 3–5 mm diam., tunics concentric, fragmenting vertically into elliptical segments. *Flowers* sometimes very small, with *tepals* (6–)7–12 (–15) mm long. *Filaments* 2–4 mm long; *anthers* 3–4 mm long. *Chromosome number,* unknown.

Flowering time. Late August to October.

Distribution. Sandy and shale slopes and flats, Cold Bokkeveld, and east through the Warm Bokkeveld and the Witteberg and Voetpadsberg, with outlying disjunct populations in the Little Karoo, the Albertinia district and Long Kloof in the southern Cape. Figure 26.

Subspecies *marlothii* has an ovate-elliptic corm with concentric tunics. This corm is typical of subgenus *Weihea* and must be viewed as the ancestral type in *G. ornithogaloides,* while the campanulate corm of subsp. *ornithogaloides* is specialized and derived. In all other features, the two subspecies are essentially identical, although there are several populations of subsp. *marlothii* on the edges of the range of this subspecies that have smaller flowers than any found in subsp. *ornithogaloides.*

The smaller flowered collections are those to the north and east of the main range for subsp. *marlothii,* which is centered in the Cold and Warm Bokkeveld. The northern extension is represented by a collection from the Koudeberg near Wuppertal (*Schlechter 8749*) and the eastern extension by collections from the Witteberg (e.g., *Compton 3806*) and from apparently disjunct populations in the Little Karoo, Albertinia district (southern Cape) and in the Long Kloof. The eastern populations are few and scattered and subsp. *marlothii* is apparently rare outside its main range. There is nothing as yet known to suggest that these eastern populations represent a distinct taxon as they are similar to several flowered plants from other localities, notably to the Schlechter and Compton collections mentioned above.

Specimens examined. SOUTH AFRICA. CAPE: 3219 (Wuppertal) Koudeberg, Wuppertal (AC), *Schlechter 8749* (B, BM, BOL, BR, E, G, H, K, L, MO, PH, PRE, S, Z); Houdenbeck, Cold Bokkeveld (AD), *Marloth 10612* (B, PRE, STE), Cold Bokkeveld, 3 mi. S of Leeurivier (CC), *Lewis 2637b* (SAM); Bokkeveld Tafelberg (CD), *Leighton s.n.* (BOL); Cold Bokkeveld, flats at De Keur, *Esterhuysen 13006* (BOL, PRE); Schoongesig, Ceres, *Hanekom 1222* (K, PRE, STE).

3319 (Worcester) 7 mi. W of Gydo Pass, Cold Bokkeveld (AA), *Hutchinson 1055* (K, NBG); Gydo, Ceres (AB), *Leipoldt 3811* (BOL); 6 mi. N of the top of Gydo Pass, *Lewis 2637a* (SAM); Groenfontein, *Barker 3115* (NBG); between Loch Lynne and Winkelhaak, *Oliver 5120* (K, MO, PRE, S, STE); Lakenvlei (BC), *Olivier s.n.* (NBG 60692); Theronsberg Pass, *De Vos 1673* (STE); Orchard Siding, Worcester, *Rogers 16570* (K), *16666* (K).

3320 (Montagu) poort N of Pienaarskloof, Ceres Div. (AA), *Acocks 23700* (PRE); Voetpadsberg, *Barker 7497* (NBG); Elandsfontein, Witteberg (AD), *Compton 3806* (BOL, NBG); farm Rietvlei, off Ouberg Pass, N of Montagu (CA), *Perry 1674* (NBG).

3321 (Ladismith) Swartberg Mts., Gamka Nature Reserve (BC), *Vlok 314* (MO).

3323 (Willowmore) Avontuur-George road, farm Arbor Nook, Pootjiesrivierhoogte (CA), *Snijman 361* (NBG).

3324 (Steytlerville) Company's Drift, Long Kloof (CC), *Fourcade 2313* (BOL, K, STE).

3421 (Riversdale) Albertinia (BA), *Erasmus 1578* (STE), *1624* (STE); Plattebosch, near Albertinia, *Muir 1810* (BOL).

WITHOUT PRECISE LOCALITY: Ceres Wild Flower Show, *Lewis s.n.* (BOL 21246).

12B. Subsp. **ornithogaloides.** FIGURE 26.

Geissorhiza flava Reichb. ex Klatt, Abh. Naturf. Ges. Halle 12: 392 (Erg. 58). 1882. TYPE: South Africa. Cape: without precise locality, *Breutel s.n.* (holotype, B).

Waitzia flava Reichb. ms., Klatt, Abh. Naturf. Ges. Halle 12: 392. 1882, in syn.

Geissorhiza ornithogaloides var. *flava* (Klatt) Foster, Contr. Gray Herb. 135: 68. 1941.

Geissorhiza romuleoides Ecklon, Topogr. Verz. Pflanzensamml. Ecklon 27. 1827, nom. nud. et ms. [*Ecklon & Zeyher Irid. 225* (51.8)].

Corm campanulate with an obliquely flattened base, 4–6 mm at widest diam., *tunics* medium brown, concentric, in two parts, with a cap, and separate basal disc, lower margins of cap serrate. *Flowers* with tepals 8–12(–18) mm long. *Filaments* 2.5–4 mm long; *anthers* 3–4.5 mm long. *Chromosome number*, $2n = 26$ (*Goldblatt 214* as *G. nana*).

Flowering time. September to October.

Distribution. Clay and sandy flats and slopes from the Paarl district east to Worcester and the Hex River Valley and south to the Caledon district. Figure 26.

As already discussed, subsp. *ornithogaloides* differs from subsp. *marlothii* only in its corms. The corms of subsp. *ornithogaloides* are campanulate with a flat base, and have a serrate lower margin. Subspecies *marlothii* has ovate-elliptic corms, tapering at both ends, a type found in most species of subgenus *Weihea*. In other features, the two subspecies are essentially identical, except that some populations of subsp. *marlothii* have smaller flowers than any found in subsp. *ornithogaloides*.

Geissorhiza flava Klatt is a name applicable to larger flowered, robust forms of *G. ornithogaloides*, and although corms are lacking from the type, it most likely is synonymous with subsp. *ornithogaloides*. Foster (1941) reduced *G. flava* to varietal rank, distinguishing it as being somewhat larger and usually 2-branched. As he comments, it tends to intergrade with the typical variety. With the considerably greater number of collections available to me, it seems clear that even this treatment is unacceptable. Variation within populations of *G. ornithogaloides* can be considerable and robust plants corresponding to *G. flava* may grow next to small slender individuals matching the lectotype of *G. ornithogaloides* (e.g., *Lewis 6052*).

Specimens examined. SOUTH AFRICA. CAPE: 3318 (Cape Town) near Hercules Pillar (DD), *Salter 4721* (BM, BOL, K), *Mathews s.n.* (Nat. Bot. Gard. 1419/30 in BOL); Agter Paarl, *Barker 404* (NBG).

3319 (Worcester) Romansrivier (AC), *Lewis 2638* (SAM); Romans River Nature Reserve, *Goldblatt 6290* (MO, WAG); Buffelsrug, Osplaats Station, NE of De Doorns (BC), *Mauve & Oliver 235* (STE); Brandvlei, sandy flats near the water (CB), *Lewis 6052* (NBG, STE); Du Toits Kloof-Stettyns Kloof, *Barker 9454* (NBG); E end of Du Toits Kloof, sandy flats, *Lewis 6043* (NBG, S), *Goldblatt 2412* (MO, NBG, S); between Du Toits Kloof and the Breede River on stony roadside, *Goldblatt 4703* (MO, NBG); road from Villiersdorp to Worcester (CD), *Goldblatt 205* (BOL), *Barker 7540* (NBG); S slope of Quaggasberg, *Mauve & Oliver 264* (STE); between Brandvlei and Villiersdorp, *Goldblatt 6202* (MO, PRE, S, WAG).

3418 (Simonstown) sandy flats between Gordons Bay and Strand (BB), *Parker 4241* (GH, NBG, K).

3419 (Caledon) between French Hoek and Villiersdorp (AA), *Lewis 2898* (SAM); Sondereinde River bridge on Villiersdorp-Caledon road (AB), *Salter 4792* (BOL, K); Caledon, *Leipoldt s.n.* (BOL); Caledon, Zwartberg and about the Baths, *Ecklon & Zeyher Irid. 225* (51.8) (B, BM, BOL, E, FI, G, GH, L, LD, MO, S, W, Z); Zwartberg, Caledon, *Zeyher 3966* (B, FI, G, K, SAM); commonage below Zwartberg, Caledon, *Guthrie s.n.* (BOL 16917); hillside above vlei, Caledon road 1 mi. from Villiersdorp turnoff, *Barker 13* (BOL, K); stony flats S of Villiersdorp at Theewater farms turnoff, *Goldblatt 4016* (MO); road from Shaws Pass to Caledon (AD), *Goldblatt 214* (BOL); Onverwacht, 19 mi. W of Riviersonderend (BA), *Acocks 22665* (PRE).

3420 (Bredasdorp) Potberg flats, De Hoop Nature Reserve (BC), *Burgers 2248* (STE).

WITHOUT PRECISE LOCALITY: Cape, *Breutel s.n.* (B "Herb. Lubeck").

13. **Geissorhiza malmesburiensis** Foster, Contr. Gray Herb. 135. 1941. TYPE: South Africa. Cape: hill near Malmesbury, 300 m, *Schlechter 1654* (holotype, B; isotypes, B, BOL, BR, L, MO, PRE, Z). FIGURE 27.

Plants small, 5–8 cm high. *Corm* campanulate with an oblique flat base, 4–6 cm at widest diam., tunics medium brown, concentric, in two parts, a campanulate cap and basal plate, the lower margins of the cap toothed. *Cataphyll* membranous, evidently often lacking. *Leaves* usually 4, the lower two or three basal, linear-filiform, more or less erect, to 1 mm wide, blade plane, the upper two or uppermost inserted on the stem at or above ground level, sheathing and inflated

below, narrow above. *Stem* erect, simple or branching from the upper leaf or leaves. *Spike* 1-flowered; *bracts* pale green, with a hyaline margin, becoming dry above, 7–11 mm long. *Flower* clear yellow, cupped; *perianth tube* ca. 4 mm long, included in the bracts; *tepals* obovate, 13–25 mm long, to 8 mm wide. *Filaments* ca. 6 mm long, erect; *anthers* 4–5 mm long, yellow. *Ovary* ca. 3 mm long, *style* dividing at the apex of the anthers, branches ca. 4 mm long, recurved. *Capsule* unknown. *Chromosome number,* $2n = 26$ (*Goldblatt 6282*).

Flowering time. September to early October.

Distribution. Restricted to the Malmesbury district. Figure 27.

When Foster (1941) described this species from a single sheet of a Schlechter collection, he was unaware of the nature of its corm. A second sheet of the type collection also at Berlin Herbarium has several corm fragments, while the only other collections of *Geissorhiza malmesburiensis,* made by Lewis in 1952 and by myself in 1981, have intact corms, and it is now clear the species has the striking corm previously thought restricted to *Geissorhiza ornithogaloides* (here subsp. *ornithogaloides*). The corm is campanulate in outline with an oblique flat base, and toothed lower margins. The corm structure bears out Foster's suggestion that *G. malmesburiensis* is closely related to *G. ornithogaloides.* The two in fact differ mainly in the size of the floral parts. *Geissorhiza malmesburiensis* has flowers much larger than any known in *G. ornithogaloides,* although all plants so far collected are rather small, slender, and few branched. Flowers of *G. malmesburiensis* have a perianth tube ca. 4 mm long and tepals 13–25 mm long but usually in the 20–25 mm range, while in *G. ornithogaloides* the perianth tube is 2–3 mm long and the tepals (6–)7–15 mm long, rarely to 18 mm, and robust plants with larger flowers are always branched and have spikes of more than one flower each.

This species is evidently extremely rare. The only known habitat, on the slopes above Malmesbury, is being developed for housing, and this population will soon be extinct. *Geissorhiza malmesburiensis* may occur elsewhere in the Malmesbury district, but collecting in this heavily agricultural area has so far failed to produce other records of the species. It must be regarded as seriously endangered and if not extinct, then on the verge of extinction.

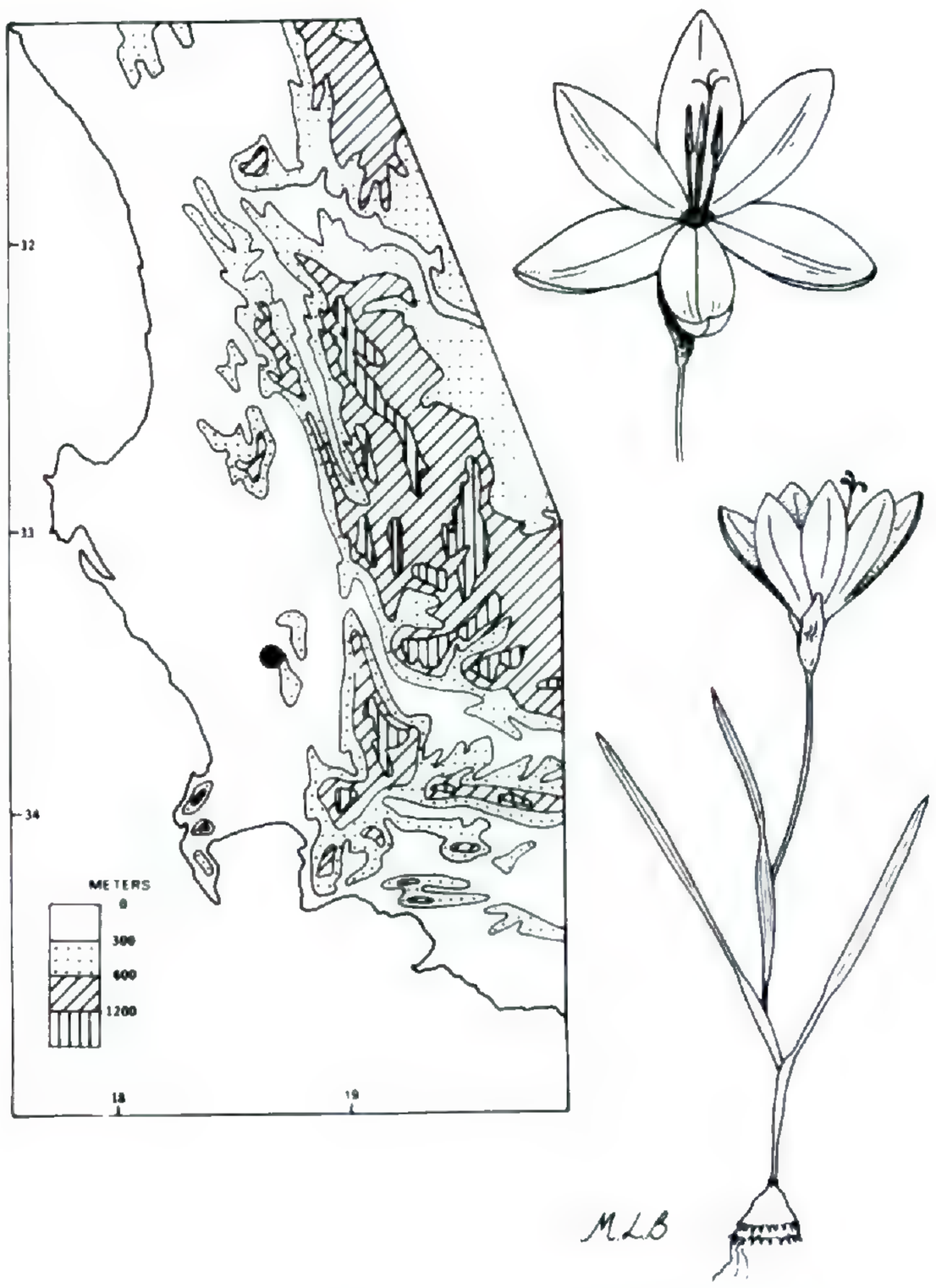


FIGURE 27. Morphology and distribution of *Geissorhiza malmesburiensis.* Habit life size; separate flower ×2 (*Goldblatt 6282,* Malmesbury Commonage).

Specimens examined. SOUTH AFRICA. CAPE: 3318 (Cape Town) Malmesbury commonage (BC), *Lewis 3633* (SAM), *Goldblatt 6282* (MO); hill near Malmesbury, 300 m, *Schlechter 1654* (B, BOL, BR, L, MO, PRE, Z).

14. Geissorhiza geminata E. Meyer ex Baker, Handb. Irid. 159. 1892, Fl. Cap. 6: 76. 1896; Foster, Contr. Gray Herb. 135: 63. 1941. TYPE: South Africa. Cape: between Slangenheuwel, Franschehoek and Donkerhoek, *Drège s.n.* "*G. geminata* EM. α" (lectotype, K, designated here; isolectotypes, B, BM, E, G, K, L, MO, P, S) [Foster (1941) failed to indicate which of the sheets at K was the "type" hence his apparent lectotypification cannot be accepted]. FIGURE 28.

Geissorhiza geminata Drège ms.; E. Meyer, Flora 26 (Beigabe): 119–187. 1844, nom. nud.

Plants (12–)16–30 cm high. *Corm* globose, more or less symmetric, obliquely flattened below, tunics concentric, light brown, fragmenting irregularly into segments, drawn into short bristles above. *Cataphyll* membranous. *Leaves* 3–5,

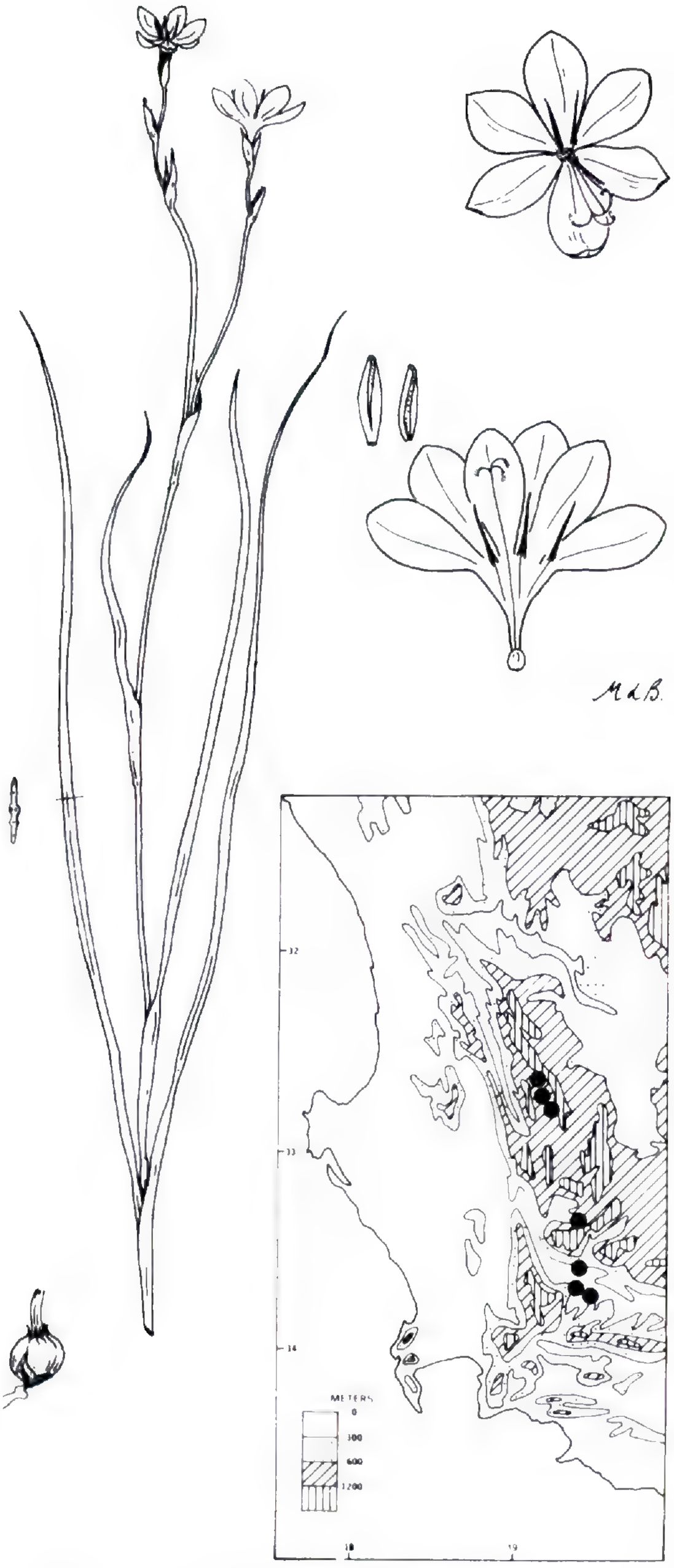


FIGURE 28. Morphology and distribution of *Geissorhiza geminata*. Habit and corm ×0.5; intact and opened flower and floral bracts life size; leaf section much enlarged (*Goldblatt 6981*, flats near Worcester).

the lower two or three basal, shorter than the stem, 1–2 mm wide, blade plane when dry, possibly inflated and terete when live in some populations, the upper leaves cauline and partly sheathing, uppermost bract-like, often vestigial. *Stem* erect, bearing leaves below and leafy bracts above, often branched and then dichotomously. *Spike* 1–3-flowered; *bracts* herbaceous, hyaline or reddish along the margins, 6–8 mm long, the inner about as long, or longer than the outer. *Flower* white (to cream), stellate, sometimes pink on the reverse of the tepals; *perianth tube* to 8 mm long, reaching the apex of the bracts or longer; *tepals* to 14 mm long, ca. 6 mm wide. *Filaments* to 4 mm long, erect; *anthers* 5 mm long. *Ovary* 1.5–3 mm long, *style* dividing at the apex of the anthers, branches ca. 4 mm long, recurved. *Capsule* unknown. *Chromosome number,* unknown.

Flowering time. September to November.

Distribution. Marshes and vleis, in sandy areas from Brandvlei north to the Cold Bokkeveld. Figure 28.

Geissorhiza geminata is a semi-aquatic species, typically found in seasonally marshy areas, sometimes in standing water. It occurs in the Worcester and Ceres districts, north into the Cold Bokkeveld. It is often confused with the superficially similar *G. brehmii* (syn. *G. teretifolia*) which also grows in aquatic habitats and has fairly large white flowers. The two species are, however, quite unrelated. *Geissorhiza brehmii* has imbricate corm tunics typical of subgenus *Geissorhiza,* while *G. geminata* has the concentric tunics of subgenus *Weihea. Geissorhiza geminata* is most probably allied to *G. setacea* and *G. ornithogaloides* (section *Weihea*), and it has the flat leaf lamina characteristic of the section. It can be distinguished by its large white flower, long perianth tube usually exserted from the bracts and also by its characteristic pattern of nearly dichotomous branching in the upper stem. This branching pattern is so distinctive that most specimens of *G. geminata* can be recognized at once from this character alone.

The name *Geissorhiza geminata* was first used by Drège on his collections of the species and the name was subsequently published by Meyer (1843) in this treatise on Drège's travels and collections. A valid description was not published until 1892 by J. G. Baker. Earlier, Vahl (1805) described an *Ixia geminata,* which is according to Lewis (1962), synonymous with *G. geminata.* It is not, however, the basionym for *G. geminata* which was treated as a new name in *Geissorhiza.* The identity of Vahl's *Ixia geminata* is unknown to me. The type specimen in the Vahl Herbarium has been lost, although a sheet, now bearing only the faint impression of a plant, still exists.

Specimens examined. SOUTH AFRICA. CAPE: 3219 (Wuppertal) Cold Bokkeveld, vlei at Leeurivier bridge (CC), *Horrocks 37* (NBG); Skoongesig, Cold Bokkeveld, *Hanekom 1269* (PRE); between Groot River and Elands Kloof, *Leipoldt 3036* (BOL), *3038* (BOL).

3319 (Worcester) near Lakenvlei (BC), *Phillips 2077* (SAM); Brandvlei (CB), *Lewis s.n.* (BOL 20414, K); near Worcester, in water, *L. Bolus s.n.* (BOL 19180), *Goldblatt 6981* (E, K, MO, NBG, PRE, S, US, WAG); Moordkuil, Worcester (CD), *Lewis 2896* (SAM); Scherpenheuwel vlei (DA), *Barker 7507* (NBG).

WITHOUT PRECISE LOCALITY: between Slangenheuwel, Franschehoek and Donkerhoek, *Drège s.n.* "*G. geminata* EM. α" (B, BM, E, G, K, L, MO, P, S); Cape of Good Hope, *Heatley 6394* (BM).

15. Geissorhiza ovalifolia Foster, Contr. Gray Herb. 135: 58. 1941. TYPE: South Africa. Cape: "Drakensteinsbergen, 4,000–5,000 ft., Oct.," *Drège s.n.* (holotype, B; isotypes, G, S).

Plants small, 3–7(–9) cm high. *Corm* ovoid, 2 mm diam., tunics concentric, papery and soft. *Cataphyll* evidently dark, membranous or becoming fibrous. *Leaves* 4–5, the lower three to four basal and prostrate, the uppermost cauline and bract-like, lanceolate-oblong, occasionally ovate, acute, 2–5 mm wide, 1–4 cm long, bearing a cormlet in the axil of one or more basal or rarely cauline leaf. *Stem* often prostrate near base, then erect, with a leaf bract in lower third to midline, rarely 1-branched. *Spike* 1–4(–6)-flowered, flexuose; *bracts* herbaceous, becoming membranous above, 4–7 mm long, the inner usually slightly shorter than the outer. *Flowers* stellate, white, yellow in the throat; *perianth tube* 2–3 mm long, widening from the base; *tepals* ovate, 6–8 mm long, to 3.5 mm wide. *Filaments* 2–3 mm long; *anthers* 1.5–3 mm. *Ovary* ca. 2 mm long, *style* dividing at the apex of the anthers, branches 1.2–2 mm long, recurved. *Capsules* ovoid, 3–5 mm long. *Chromosome number,* unknown.

Flowering time. Late September to mid-November.

Distribution. Mountains of the western Cape from French Hoek north to Visgat and the Twenty Four Rivers Mountains, usually in shaded sites in damp moss. Figure 29.

Geissorhiza ovalifolia is a poorly known mountain species of damp shady sites in mossy banks, cracks in cliffs and rocky ledges, or under boulders. It is often confused with the more widespread and common *G. bolusii* which occurs in similar habitats in the Cape mountains. *Geissorhiza ovalifolia* is evidently sexually fertile, and capsules develop rapidly after blooming. Unfortunately, few mature plants are known. It also produces a cormlet in one or two basal or rarely cauline leaf axils which gives it a characteristic appearance. In contrast, *G. bolusii* is a triploid, sexually sterile species, and it produces cormlets in all basal and cauline leaf axils, and also in the fertile bract axils after flowering. The two can sometimes also be distinguished by the number of cauline leaf bracts, one being characteristic of *G. ovalifolia* while there are usually several in *G. bolusii.* This distinction does not always hold, and some specimens of *G. bolusii* may also have a single leaf bract on the stem.

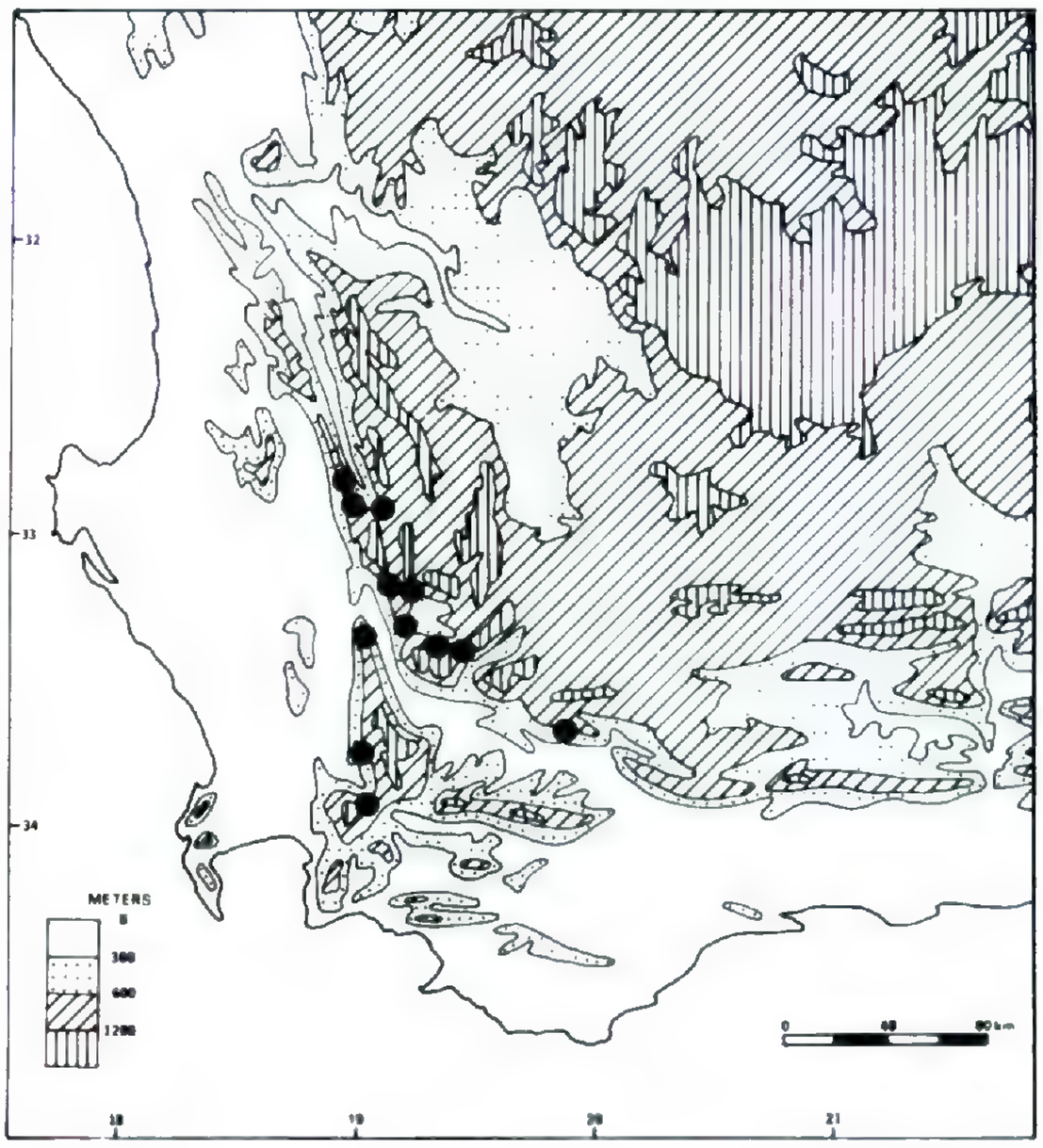


FIGURE 29. Distribution of *Geissorhiza ovalifolia.*

In some specimens, the slightly darker yellow color in the perianth tube and throat gradually intensifies with age, and in the early nineteenth century collections of Drège, and Ecklon and Zeyher, it has turned dark blue. This has been the cause of some taxonomic confusion and Foster (1941) believed the dark center to be a significant taxonomic feature of *G. ovalifolia.*

Specimens examined. SOUTH AFRICA. CAPE: 3319 (Worcester) Twenty Four Rivers Mts., damp shady spots (AA), *Esterhuysen 16164* (BOL, PRE); Visgat, *Stokoe s.n.* (SAM 63131); Groot Winterhoek farm, mts. behind Porterville, *Boucher 1902* (PRE, STE); near Porterville, *Edwards s.n.* (BOL); Witsenberg, Inkruip Ridge above De Eiker, *Esterhuysen 33612* (BOL, K, MO, PRE, S, US); mts. W of Gydo Pass, *Hutchinson*

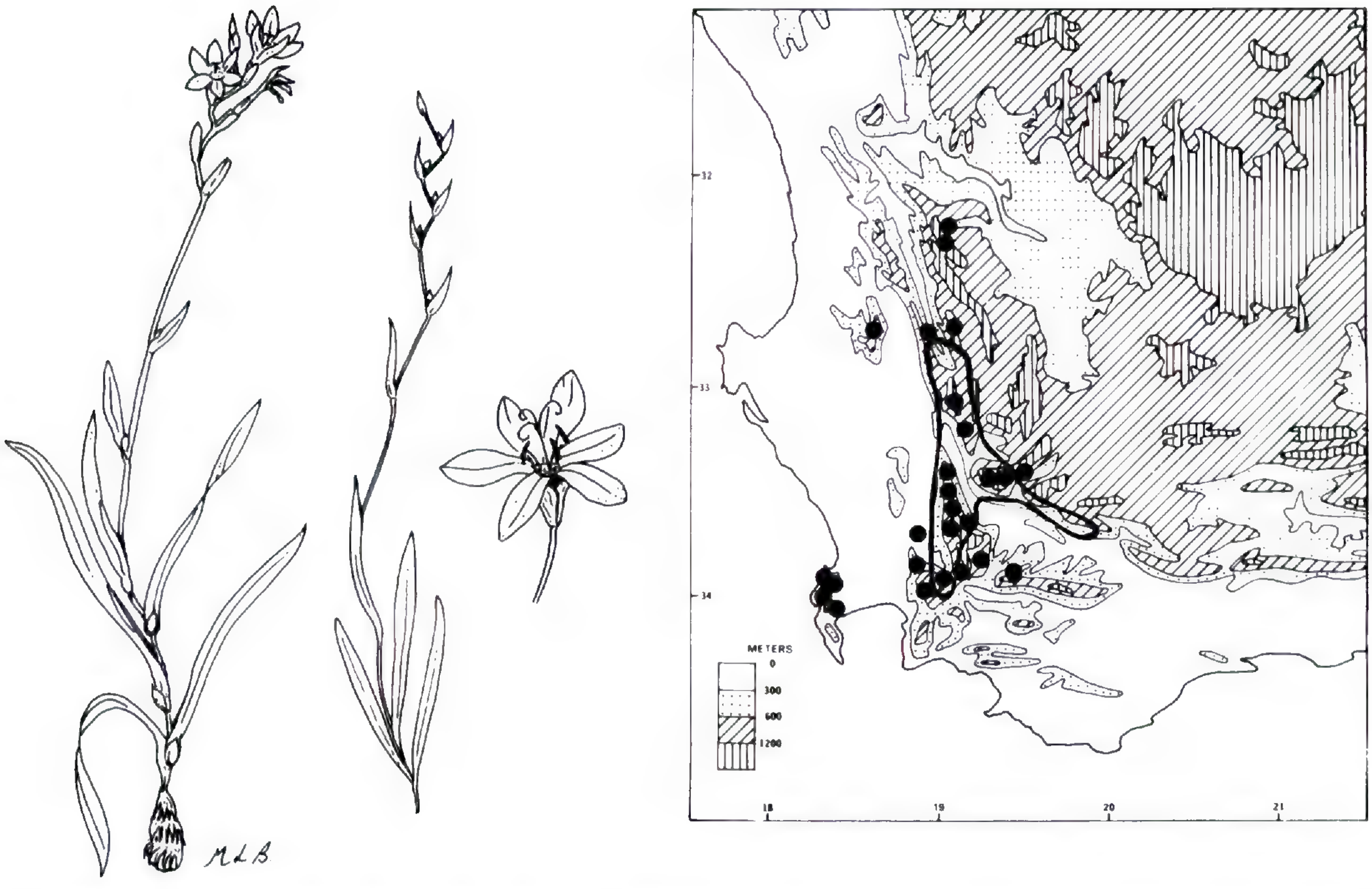


FIGURE 30. Morphology and distribution of *Geissorhiza bolusii* with the range of the closely allied, sexually fertile *G. ovalifolia* outlined. Flowering plant ×0.5; sterile plant and flower life size (*Esterhuysen 35281A*, Simonsberg).

1013 (K); Hartebeeskloof, S slopes of Vaalboskloofberg (AB), *Oliver 5162* (STE); Worcester, "beim waterfall" (AC), *Ecklon & Zeyher Irid. 223* (B, FI, G, LD, MO, S); Hex River Mts., Milner Ridge Peak (AD), *Esterhuysen 9341* (BOL); Michells Pass, *Esterhuysen 6202* (BOL), *Compton 11934* (NBG); Ceres side of Michells Pass, *Thorne s.n.* (MO, SAM 51236); rugged slopes above Merweda, E of Eselfontein, *Esterhuysen 32678* (BOL, K, MO, PRE); French Hoek Forest Reserve near Bushmans Castle (CC), *Salter 6869* (BOL, SAM); Langeberg, above Berg-en-dal farm, ca. 2,000 ft., steep S facing slopes and cliffs (DB), *Esterhuysen 35683* (K, MO, NBG, PRE, WAG).

3419 (Simonstown) Helderberg, Somerset West (BB), *Dummer 590* (E).

WITHOUT PRECISE LOCALITY: Witsenberg, Tygerkloof, *Zeyher s.n.* (SAM 20889), *Drège s.n.* (B).

16. Geissorhiza bolusii Baker, Handb. Irid. 158. 1892, Fl. Cap 6: 75. 1896; Foster, Contr. Gray Herb. 135: 57–58. 1941; Lewis, Fl. Cape Penins. 254. 1950. TYPE: South Africa. Cape: Du Toits Kloof, 2,300 ft., *H. Bolus s.n.* [lectotype, BOL 5247 in K, effectively designated by Foster (1941); isolectotype, BOL]. FIGURE 30.

Geissorhiza rupestris Schltr., Bot. Jahrb. Syst. 27: 98. 1899; Foster, Contr. Gray Herb. 135: 57. 1941. TYPE: South Africa. Cape: mts. above Bains Kloof, 2,400 ft., *Schlechter 9167* [lectotype, B, designated by Foster (1941); isolectotypes, B, BM, BOL, E, G, H, K, L, MO, PH, PRE, Z].

Geissorhiza dregei Baker, Handb. Irid. 158. 1892, Fl. Cap. 6: 74. 1896; Foster, Contr. Gray Herb. 135: 56. 1941. TYPE: South Africa. Cape: Paarl Mts., *Drège s.n.* "*G. secunda* β Ker α" [lectotype, K, effectively designated by Foster (1941); isolectotypes, BM, E, G, K, L, MO]; without locality, *Thunberg s.n.* (syntype, Herb. Burman G = *G. parva*); Olifantshoek, *Ecklon & Zeyher Irid. 221* (syntype, SAM = *G. parva*).

Geissorhiza tabularis Ecklon ms. (*Ecklon 311*).

Plants 3–8(–11) cm high. *Corm* more or less ellipsoid, 2–4 mm diam. at widest, tunics pale, concentric, brittle-papery, notched below into sections, and drawn into points above. *Cataphyll* transparent, membranous. *Leaves* 2–5, basal, ensiform to lanceolate, acute, usually prostrate, blade flat, the stem also bearing leafy bracts. *Stem* usually prostrate at the base, erect above, occasionally branched, with a few to several leafy bracts, bearing a small cormlet in the axil of each leaf and bract. *Spike* 2–8-flowered, or flowers all aborted but floral bracts subtending cormlets; *bracts* green, 3–6(–10) mm long, the inner about as long or longer than the outer in those subtending flowers, much smaller where flowers

aborted, a cormlet produced in the axil of each sterile bract and, after flowering, in the axils of the floral bracts. *Flowers* stellate, white (or not produced on some plants); *perianth tube* infundibuliform, 3–4 cm long, reaching apex, or slightly exserted from bracts; *tepals* 7–10 mm long, spreading, ovate, 2–3 mm wide. *Filaments* 3–4 mm long; *anthers* 2–3 mm long. *Ovary* 3–4 mm long, *style* dividing near the apex of the anthers, branches ca. 1.5 mm long, recurved. *Capsules* and seeds never developed. *Chromosome number,* $2n = 39$ (*Goldblatt 458, 515, 6444, Goldblatt s.n.* no voucher, High Noon Mts.; *Esterhuysen 35281A*).

Flowering time. October to December (to January).

Distribution. Mountains along the western Cape coast and interior from the Cape Peninsula to the Cedarberg, shady south-facing slopes, rock cracks, often in damp sites with moss. Figure 30.

Geissorhiza bolusii is a poorly collected, yet widespread species, common in suitable habitats in the mountains of the western Cape. It favors cool damp sites in shallow soil under rocks or in cracks of south-facing cliffs or along watercourses, and it is often associated with moss. The species is unusual, being triploid, $2n = 39$ (counts from five separate populations from different parts of its range), and it never reproduces by seed. Instead a small cormlet develops in the axil of each leaf and stem bract. Some flowering stems produce no flowers, but a cormlet in the axil of each flower bract. Other stems produce small white flowers, but no capsules, and a cormlet later develops in place of each aborted ovary. The presence of these two kinds of stems, flowering and vegetative, is one characteristic feature of *G. bolusii,* and most collections comprise plants of both kinds, including the type collections of *G. bolusii* and *G. rupestris,* the latter reduced to synonymy here. One of the three type collections of *G. dregei, Drège s.n.* from Paarl Mountain, chosen here as lectotype for this species, also exhibits this characteristic. The two other type collections consist of rather poor specimens of *G. parva.* Thus *G. dregei,* recognized as distinct by Foster (1941), is likewise reduced to synonymy in *G. bolusii.*

Geissorhiza bolusii is probably most closely related to *G. ovalifolia* which grows in similar habitats and also has small, white flowers. *Geissorhiza ovalifolia* usually has none or only one cauline leaf or bract, and produces one or few cormlets in its leaf axils. In *G. ovalifolia,* fruit development is evidently fairly rapid and immature capsules can be seen in some collections in which fading blooms are present at the ends of spikes.

Specimens examined. SOUTH AFRICA. CAPE: 3218 (Clanwilliam) Piketberg (D-), *Barker 7856* (NBG); Gryskop, Piketberg, 3,500 ft. (DC), *Pillans 7400* (BOL); Zebrakop, Piketberg, 3,000–4,000 ft., *Esterhuysen 35805* (MO).

3219 (Wuppertal) N Cedarberg at Koupoort (AA), *Esterhuysen 12188* (BOL); Cedarberg, Middelberg vlakte, under boulders (AC), *Goldblatt 5135* (K, MO, PRE, S); Elandskloof, rock ledges (CA), *Bond 677* (NBG); Hexberg, Cold Bokkeveld Mts., *Goldblatt 7114* (K, MO); Warm Baths, Olifants River Valley, *Edwards s.n.* (BOL 14430); Bo-Boskloof, Cold Bokkeveld (CC-CD), *Rourke 651* (NBG).

3318 (Cape Town) Table Mt., S aspect (CD), *H. Bolus 4617* (BOL); Table Mt., *Ecklon 311* (G, K, M, PRE, S), *Marloth 8041* (PRE); Platteklip Gorge, *Dümmer 858* (E); Devils Peak, *Wolley Dod 488* (BOL); Cecilia, *Barker 20181* (NBG); Lions Head, damp places near chains, *Rennie s.n.* (CT); Paarl Mt. (DB), *Drège s.n.* (G, K, MO); Jonkershoek, below first Ridge Peak, 2,900 ft. (DD), *Kerfoot 6097* (NBG); Simonsberg, kloof near Helshoogte, *Esterhuysen 35281A* (MO).

3319 (Worcester) Groot Winterhoek, moist rocks (AA), *Marloth 2329* (PRE); Witsenberg (AC), *Zeyher 3958* (SAM); shady damp rocks, upper Tulbagh Waterfall, *Burgers 2586* (STE); Milner Peak, Hex River Mts. (AD), *Esterhuysen 14240* (BOL); Hex River valley (BC), *Davidson 116* (SAM), *53* (SAM); Bains Kloof (CA), *Schlechter 9167* (B, BM, BOL, E, G, H, K, L, MO, PH, PRE, Z), *Esterhuysen 32723* (BOL), *Goldblatt 458* (BOL), *Kies 380* (PRE), *L. Bolus s.n.* (BOL), *Barker 4250* (NBG, W); Cossacks, Slanghoek Mts., ca. 4,000 ft., *Esterhuysen 35823* (C, K, WAG); Sneeukop Mts., Wellington, *Thorne s.n.* (SAM 46558); Du Toits Kloof, *Loubser 861* (NBG), *H. Bolus 5247* (BOL, K); Slanghoek Mts., *Esterhuysen 9454* (BOL); Waaihoek Peak, damp bank (CB), *Esterhuysen 18190* (BOL); French Hoek Pass (CC), *Barker 4910* (BOL); Jonaskop, Riviersonderend Mts., under rock overhang (DC), *Goldblatt 6444* (MO, PRE).

3418 (Simonstown) slopes of Constantiaberg (AB), *Lewis 1569* (SAM); Constantiaberg, *Compton 14171* (NBG), *Wolley Dod 1933* (K); near Constantia corner, *Lewis 1488* (NBG).

17. Geissorhiza parva Baker, Kew Bull. 1906: 26. 1906; Foster, Contr. Gray Herb. 135: 60. 1941. TYPE: South Africa. Cape: Houw Hoek, *Penther 723* (holotype, K). FIGURE 31.

Ixia excisa L. f., Suppl. Pl. 92. 1782; Thunb., Diss. de *Ixia* no. 24. 1783, pro parte excl. *Thunberg s.n.* "*Ixia excisa α*" [lectotype of *I. excisa* L. f. (Goldblatt, 1983) = *G. ovata* (Burm. f.) Asch. & Graeb.]; *Thunberg s.n.* "*Ixia excisa β*" (syntype, UPS = *G. parva*).

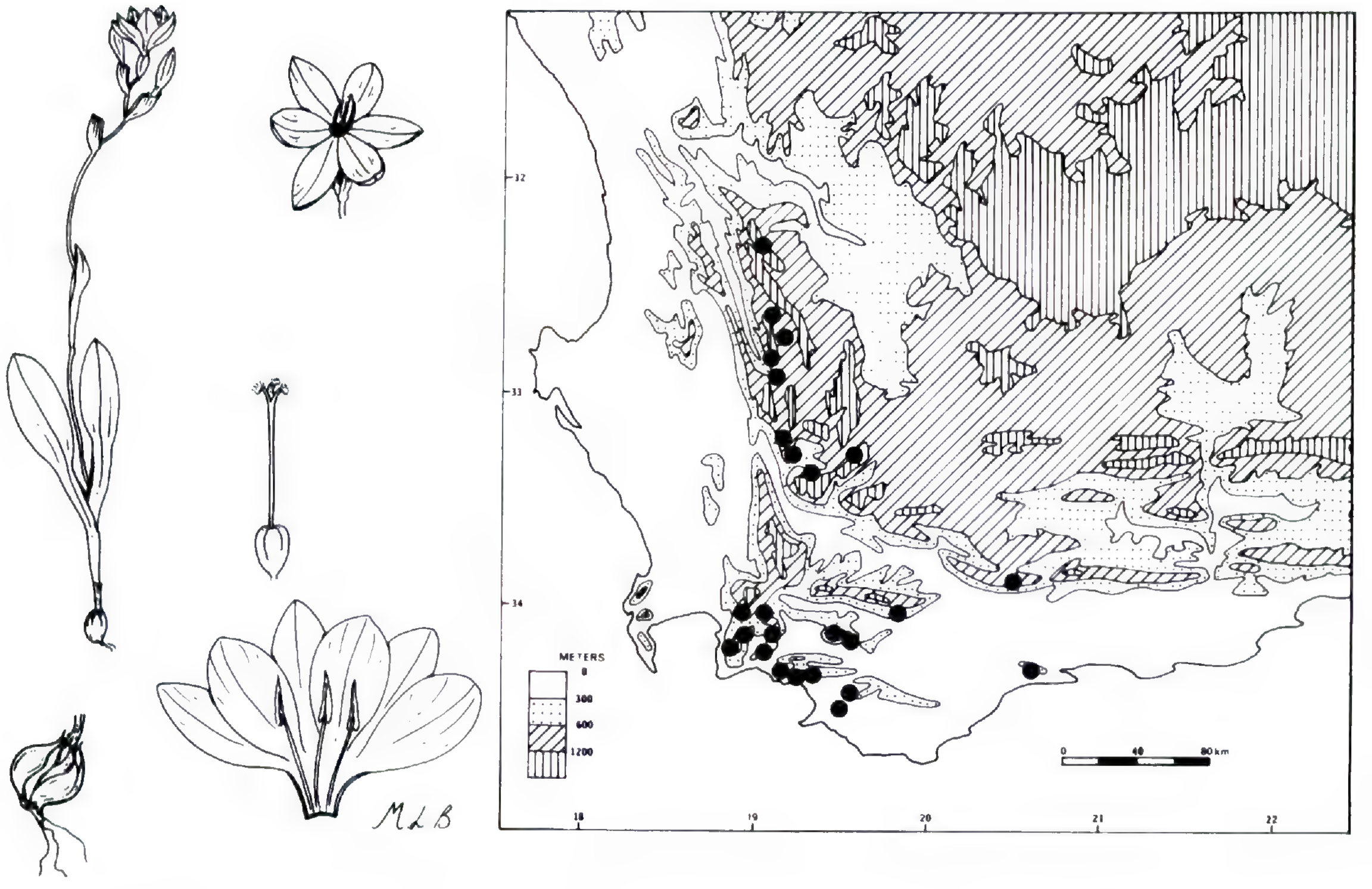


FIGURE 31. Morphology and distribution of *Geissorhiza parva*. Habit ×0.5; corm, flower, and gynoecium life size; opened flower ×2 (*Goldblatt 5897*, Caledon Zwartberg).

Geissorhiza dregei Baker, Handb. Irid. 158. 1892, Fl. Cap. 6: 74. 1896, pro parte excl. *Drège s.n.* "*G. secunda* β Ker α" (lectotype of *G. dregei* = *G. bolusii* Baker).

Geissorhiza tabularis Ecklon ms. [*Ecklon & Zeyher Irid. 222* (90.9)].

Plants small, 4–7(–12) cm high. *Corm* ovoid-conic, 3–5 mm diam., asymmetric, obliquely flattened towards base, the flat part extending downwards shortly, tunics dark brown, concentric, the layers firm textured, fragmenting irregularly. *Cataphyll* membranous brown, usually persistent and accumulating around the base. *Leaves* 3–4, all basal or the uppermost cauline, 1.5–2(–4.5) cm long, prostrate or inclined, much shorter than the stem, ensiform to oblong, rarely linear, occasionally ovate, usually minutely red-dotted or streaked, acute or obtuse, margins occasionally ciliate to papillose towards the apex. *Stem* smooth, erect above, often prostrate for a short distance at the base, simple or rarely branched, flexed above the cauline leaf. *Spike* (1–)2–6-flowered; *bracts* herbaceous, usually red on the margins, 4–6(–8) mm long, the inner slightly shorter than the outer. *Flower* stellate, creamy white to pale yellow; *perianth tube* 3–4 mm long, included or just exserted from the bracts, gradually widening from the base; *tepals* extended horizontally, more or less ovate, 6–8 mm long, 2.5–3.5 mm wide. *Filaments* ca. 2 mm long, erect; *anthers* 2–2.5 mm long, pollen yellow. *Ovary* ca. 2 mm long, *style* dividing at the apex of the anthers, branches 1.5–2 mm long, recurved. *Capsule* globose to oblong, 3–7 mm long. *Chromosome number,* unknown.

Flowering time. Mid-August to October (to early December at high altitudes).

Distribution. Sandy and often very thin mountain soils in the southwestern Cape, extending from the Cedarberg south to the Langeberg near Swellendam; mainly montane at middle to upper elevations but occasionally at low altitudes near the coast in the Caledon district. Figure 31.

Geissorhiza parva is clearly closely allied to *G. ovata,* a species similar in habit with short prostrate or semi-prostrate leaves and a long perianth tube, but larger in all features and having particularly long-tubed white flowers, marked red at the base of the tepals and on the reverse of the tepals and tube. The difference in size, flower

color, and length of the perianth tube in the two species makes confusion unlikely. *Geissorhiza parva* sometimes grows in open soil, occasionally together with *G. ovata,* but more often on thin soil on wet rocky pavement or on rocks in damp moss. It has a wide range, extending from the Cedarberg southwards to the Caledon district and east to the Langeberg near Swellendam. Populations occurring north of the Hex River Mountains can usually be distinguished by having four leaves, in contrast to the southern populations which normally have only three. The difference is not without exception, e.g., *Stokoe s.n.* from the Riviersonderend Mountains in the south, and *Esterhuysen 35719* from the Hex River Mountains to the north, consist of plants with either three or four leaves.

Some northern populations of *Geissorhiza parva* can be difficult to distinguish from the related *G. ovalifolia.* This species has white flowers, soft-textured leaves, and usually an axillary cormlet near ground level. The two species can usually be separated by a combination of these characters.

Specimens from the Commonage below the Zwartberg at Caledon, *Guthrie s.n.,* are probably hybrid with *Geissorhiza ovata.* Some individuals of this collection have very large flowers with the reverse of the outer tepals flushed red. The flowers have tepals to 13 mm long and a tube as long as 6 mm, a size intermediate between *G. parva* and *G. ovata.*

Specimens examined. SOUTH AFRICA. CAPE: 3219 (Wuppertal) Cedarberg, Middelberg (AC), *Goldblatt 5137* (MO, NBG); Elands Kloof (CA), *Lewis s.n.* (BOL 31893), *Barker 3087* (NBG); Cold Bokkeveld, 33.5 km E of Citrusdal, *Goldblatt 4203* (K, MO); Olifants River Valley, Grootfontein above the Toorgat (CC), *Oliver 3973* (K, PRE, STE); Hexberg, Cold Bokkeveld Mts., 4,000 ft., *Goldblatt 7115* (MO, PRE); Cold Bokkeveld, Wabooms River-Ysterfontein (CD), *Lewis 2644* (SAM); E side of Bokkeveld Sneeukop, after fire, in wet sand, *Esterhuysen 36126* (BOL, K, MO, PRE, S, US, WAG).

3319 (Worcester) Visgat (AA), *Stokoe s.n.* (SAM 63130); Michells Pass (AD), *Esterhuysen 6145* (BOL); near reservoir, Ceres, *Guthrie s.n.* (BOL 17233); Skurfdeberg, shallow damp soil over flat rock, *Esterhuysen 21869A* (BOL); sandy flats, foot of Skurweberg, Agterwitsenberg vlakte, *Goldblatt 4426* (MO); Matroosberg, 5,000 ft., shallow muddy soil (BC), *Esterhuysen 35719* (BOL, K, MO, PRE, S).

3320 (Montagu) near base of Crown Mt., Swellendam (CD), *Wurts 282* (NBG).

3418 (Simonstown) Hottentots Holland, Moordenaarskop (BB), *Esterhuysen 9131* (BOL); Rockview Dam site, Kogelberg, *Snijman 550* (NBG); Kogelberg Forest Reserve (BD), *Boucher 1942* (PRE, STE); Platteberg, *Stokoe s.n.* (SAM 61723).

3419 (Caledon) flats E of Viljoens Pass (AA), *Davis s.n.* (SAM 61726), *Stokoe s.n.* (SAM 61724); Viljoens Pass, *Stokoe s.n.* (SAM 49600); Lebanon State Forest, Jakkalsrivier Catchment II, moist path in peaty soil, *Haynes 1243* (STE); Houw Hoek Pass, near Bot River, *van Niekerk 785* (BOL); Caledon Zwartberg (AB), *Goldblatt 5897* (K, MO, NBG); Zwartberg near Caledon, *Galpin 4675* (K, PRE); Caledon, commonage below Zwartberg, *Guthrie 16916* (BOL); Highlands Forest Reserve, wet flats (AC), *Goldblatt 4779A* (MO); Hawston, sand hills near lagoon, *Walgate 1087* (BOL); Vogelgat, cleared path at 1,500 ft. (AD), *Goldblatt 5348* (MO); Vogelgat, roads end, 410 m, *Williams 2859* (NBG); 8 mi. from Stanford on road to Elim, *Gillett 4499* (BOL, BR, MO); Riviersonderend Mts. (BA-BB), *Stokoe s.n.* (SAM 63482); Swellendam, "am Ufer des Riviersondereinde bei Appelskraal" (BB), *Ecklon & Zeyher Irid. 222* (90.9) (B, FI, G, LD, MO); Olifantshoek, *Ecklon & Zeyher Irid. 221* (K, SAM); 2 mi. N of Papiesvlei (BC), *Acocks 22868* (K, PRE); Salmonsdam Nature Reserve, *Goldblatt 437* (BOL); Sandys Glen (BD), *Goldblatt 4849* (K, MO, NBG); flats near Baardscheerdersbos (DA), *Lewis 6007* (NBG).

3420 (Bredasdorp) Potteberg, De Hoop (BC), *Burgers 2247* (PRE, STE).

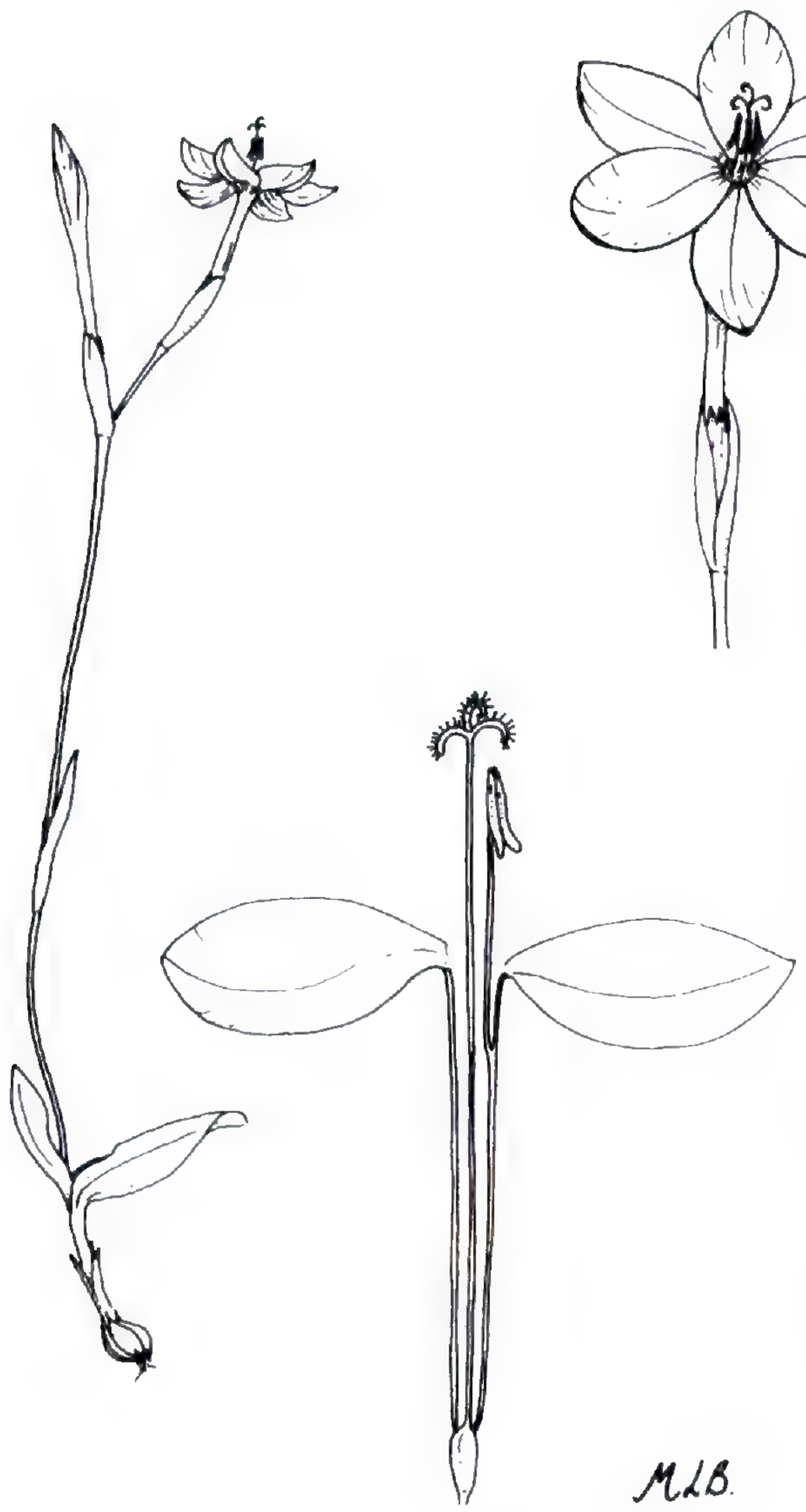
WITHOUT PRECISE LOCALITY: Cape of Good Hope, *Herb. Burman s.n.* (G).

18. Geissorhiza ovata (Burm. f.) Asch. & Graeb., Syn. Mitteleur. Fl. 3: 540. 1906; Foster, Contr. Gray Herb. 135: 59. 1941; Lewis, Fl. Cape Penins. 254. 1950. *Ixia ovata* Burm. f., Fl. Cap. Prod. 1. 1768. TYPE: South Africa. Cape: precise locality not known, *Burman s.n.* (holotype, Herb. Burman G). FIGURE 32.

Ixia excisa L. f., Suppl. Pl. 92. 1782, Thunb., Diss. de *Ixia* no. 24: 151. 1783. *Geissorhiza excisa* (L. f.) Ker, Ann. Bot. (König & Sims) 1: 224. 1804; Baker, Handb. Irid. 159. 1892, Fl. Cap. 6: 76. 1896. TYPE: South Africa. Cape: exact locality unknown, *Thunberg s.n.* "*Ixia excisa* α" [lectotype, Herb. Thunb. 951 UPS, effectively designated by Brown (1928); isolectotypes, S "Herb. Montin," "Herb. Castrom," "Herb. Swartz"]; "*Ixia excisa* β" (syntype, Herb. Thunb. 952 UPS).

Weihea excisa (Burm. f.) Ecklon, Topogr. Verz. Pflanzensamml. Ecklon 22. 1827, comb. illeg. gen. non. val. descr.

Plants 6–15 cm high. *Corm* asymmetric, ovoid, obliquely flattened below, the flat part extending shortly downwards, tunics light to dark brown, concentric, drawn into points above. *Cataphyll* dry, brown, papyraceous. *Leaves* 2–3, the upper often bract-like and inserted on upper part of the stem, the lower two basal, prostrate or inclined, much shorter than stem (1–)1.5–3(–6) cm long, 5–12(–14) mm wide, ovate-oblong, acute or obtuse, the margins usually ciliate, sometimes the blade also ciliate-pubescent on the veins (rarely



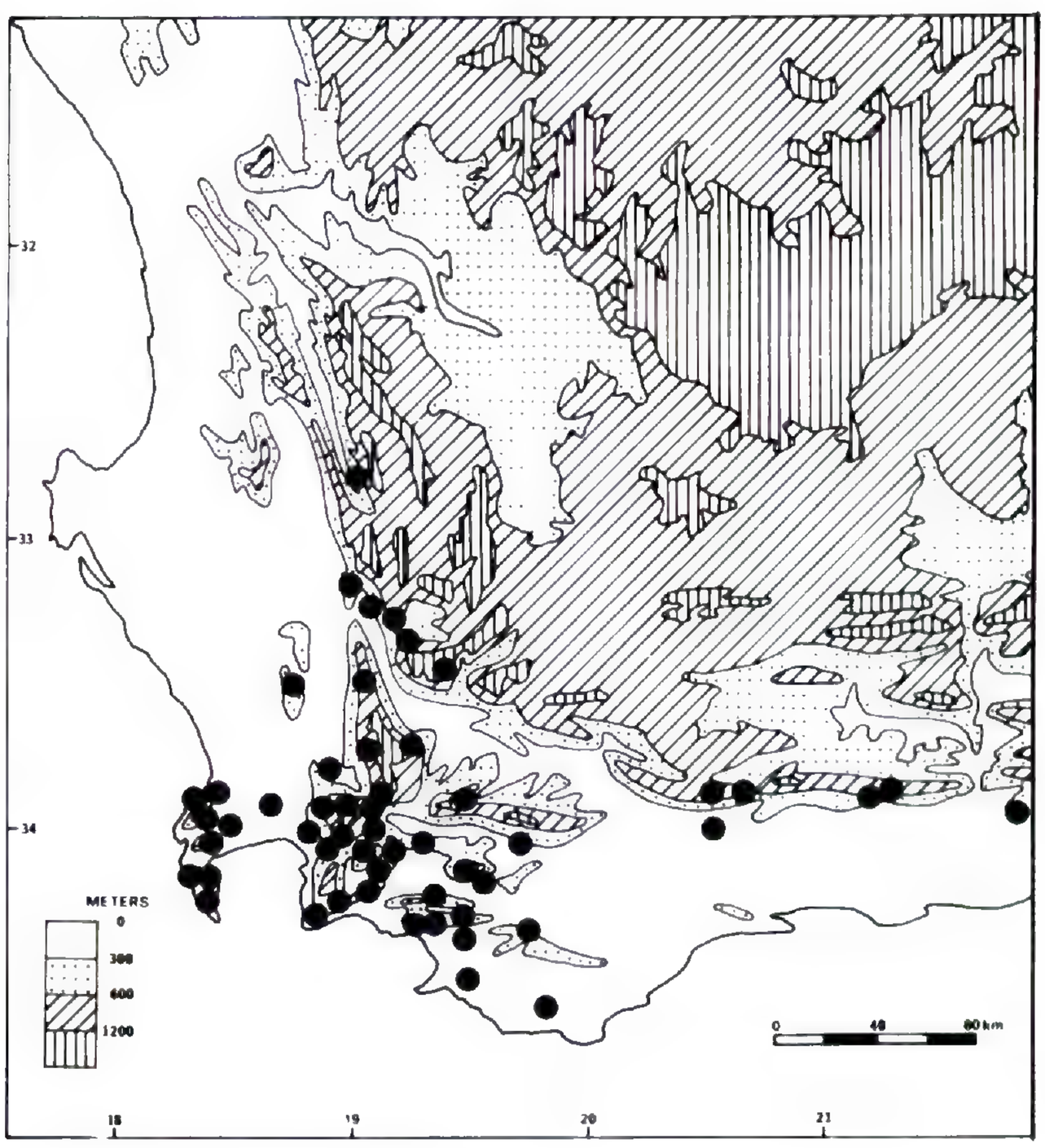


FIGURE 32. Morphology and distribution of *Geissorhiza ovata*. Habit ×0.5; flower life size; section of flower ×1.5 (*Goldblatt 5879*, Jonaskop).

pubescent throughout—*Thomas s.n.*—NBG 60659), frequently minutely brown-pellucid dotted throughout, or only towards the edges, margins thickened, often reddish. *Stem* erect above, often prostrate for a short distance at the base, unbranched. *Spike* (1–)2–6-flowered; *bracts* herbaceous, often brown dotted, 7–10(–12) mm long, the inner slightly shorter than the outer. *Flower* hypocrateriform, white or pale pink above with red marks at the base of the tepals, dark red (to brownish) on the reverse, actinomorphic; *perianth tube* cylindric, 10–18(–30) mm long, well-exserted from the bracts; *tepals* extended horizontally, lanceolate-obovate, (7–)10–13 mm long, (3.5–)5–7 mm wide. *Filaments* exserted from the tube, sometimes to 5 mm, erect; *anthers* 2–4 mm long. *Ovary* 2–3 mm long, *style* dividing at or near the apex of the anthers, branches 1.5–2 mm long, recurved. *Capsule* 6–8 mm long, rotund. *Chromosome number*, $2n = 26$ (*Goldblatt 217*).

Flowering time. (Late July to) August to October.

Distribution. Sandy mountain soils in the southwestern Cape, extending from the Cape Peninsula north to the Olifants River Mountains and east to Garcias Pass in the Langeberg; mainly montane at middle to upper elevations but also at low altitudes near the coast; usually very common after fires. Figure 32.

Geissorhiza ovata is a fairly common southwestern Cape species, especially frequent in mountain habitats after a veld fire the previous summer. It is very distinctive, having a pair of ovate or oblong, obtuse leaves prostrate or nearly so, and an erect stem with unusually long-tubed and large, white flowers marked with red in the center and on the reverse of the tepals.

It is clearly allied to *Geissorhiza parva*, a dwarf species with small yellowish cream flowers which grows on thin soil on wet rocks or moss banks, or in open soil, sometimes together with *G. ovata*. The two species are similar in their habit, having short, prostrate or semi-prostrate leaves and flowers with a long well-developed perianth

tube, although the tube of *G. ovata* is considerably longer than that of *G. parva.*

The species is quite variable and as treated here comprises several unusual forms that should be mentioned. Collections from the Klein River Mountains, especially *Ecklon & Zeyher Irid. 219* and *Stokoe s.n.* (SAM 55713, 59841), have an unusually long perianth tube, 20–30 mm long. In contrast, some collections from the Sir Lowrys Pass-Nuweberg area have a very short perianth tube only 7–10 mm long (*Compton 9205*, *Guthrie 2530*). Plants from near the eastern end of its range (*Muir 5018*—Slang River, Swellendam) have the smallest tepals, ca. 7 mm long, of any population of the species although the perianth tube is of normal length. A hairy leaved form has been recorded from Fairfield, Caledon (*Thomas s.n.*, NBG 60659). None of these variants seems worth taxonomic recognition as they do not differ sufficiently from the more common and typical form of *G. ovata* and are connected by specimens intermediate in these extreme characters to more typical forms.

Although *Ixia ovata* Burm. f. was the earliest name for *Geissorhiza ovata,* having been described in 1768, the later synonym *I. excisa* L. f. was more frequently used and when Ker (1804) transferred the species to *Geissorhiza,* he used the later synonym in the combination despite the fact that he knew and cited the earlier *I. ovata. Geissorhiza excisa* was the name used for the species throughout the nineteenth century, until Ascherson and Graebner made the combination *G. ovata* in 1906.

Specimens examined. SOUTH AFRICA. CAPE: 3219 (Wuppertal) Grasruggens, Olifants River Mts. (CC), *Oliver 3990* (STE).

3318 (Cape Town) Lions Head (CD), *Zeyher s.n.* (SAM 20882), *Pappe s.n.* (BM); Camps Bay, *Zeyher 30* (SAM), *Cassidy 285* (BOL, NBG); Zonnebloem, *Zeyher 80* (B); Table Mt., *Ecklon 831* (B, E, G, K, S, Z), *Rehmann 593* (BM, BR, Z), *Prior s.n.* (Z), *Scott Eliott s.n.* (E), *Alexander s.n.* (K); Weather Station, Table Mt., *Werdermann & Oberdieck 54* (B); Table Mt., above Klaasenbosch, *H. Bolus 4704* (BM, BOL, GH, K, M, NBG); slopes of Devils Peak, *MacOwan s.n. in Herb. Norm. Austr. Afr. 259* (B, BM, G, GH, K, SAM, Z); Table Mt., lower plateau, *Lewis 4797* (NBG); Newlands, *Wilms 3707* (B, BM, K); N slopes of Paardeberg (CA), *Goldblatt 648* (BOL); Langverwacht, above Kuils Rivier (DC), *Oliver 4369* (PRE, STE); Jonkershoek, Jakkalsvlei (DD), *Taylor 5065* (PRE, STE); Swartboskloof, Jonkershoek Valley, *Lewis 1660* (BOL, SAM); Simonsberg, moist shady rocks, *Compton 14194* (NBG); Stellenbosch flats, *Garside 280* (K); Stellenbosch, *Prior s.n.* (K).

3319 (Worcester), Summit, Roodezand Mts. (AA), *Andreae 613* (STE); lower slopes of the Witsenberg (AC), *Leighton 1339* (BOL); Tulbagh, *Grant 2471* (BOL, WAG); Michells Pass (AD), *Compton 11946* (NBG); Bains Kloof, W slope (CA), *Lewis s.n.* (BOL); Bains Kloof, *Compton 17494* (NBG), *Hafstrom & Lindeberg s.n.* (S); Baviaans Kloof, above Waterfall, *Leighton 1356* (BOL, PRE); Brandwacht Mts. (CB), *Esterhuysen 8200* (BOL); French Hoek Peak, 4,500 ft. (CC), *Compton 19856* (NBG); vleis on Wemmershoek Mts., 4,000–5,000 ft., *Wasserfall 512* (NBG); French Hoek, *Phillips 1311* (SAM); French Hoek Pass, summit ridge of Middagkransberg, *Boucher 2391* (PRE, STE); farm Stettyn, 15 mi. S of Worcester (CD), *Leipoldt 3584* (BOL); Jonas Kop, N slopes, 3,000–4,000 ft. (DC), *Goldblatt 5897* (MO); Jonas Kop, S slopes, 5,200 ft., *Thompson 136* (STE).

3320 (Montagu) Swellendam Mts. (CD), *Galpin 4677* (PRE); forest path below 10 O'Clock Peak, *Wurts 359* (NBG); Tradouw Pass (DC), *Martin 398* (NBG), *Copejans 1034* (BR).

3321 (Ladismith) Garcias Pass (CC), *H. Bolus s.n.* (BOL), *Phillips 380* (SAM), *Galpin 4676* (K, PRE); Gysmanshoek Pass, Riversdale, *Hugo 2707* (STE).

3322 (Oudtshoorn) Ruytersbosch, bushy hillside (CC), *van Niekerk 130* (BOL); Kammanassie Mts. (DB), *Viviers & Vlok s.n.* (MO).

3418 (Simonstown) Hout Bay Nek (AB), *Salter 6813* (BOL); Orange Kloof, *Wolley Dod 523* (BOL); E slope of Constantiaberg, *Schlechter 1458* (B, BM, G, H, W, Z); Vlakkenberg, *Compton 20184* (NBG), *Wolley Dod 1697* (BM); Redhill, *Taylor 1550* (SAM); Simon's Bay, *Wright s.n.* (GH, K, P); Cape Point Reserve, below Ou Kanon (AD), *Taylor 7349* (STE); Patrysvlei, *Wolley Dod 2989* (BOL); Sir Lowrys Pass (BB), *Stokoe s.n.* (SAM 49614), *Werdermann & Oberdieck 181* (B, K, PRE); Helderberg, Somerset West, *Parker 3920* (BOL, GH, K, NBG); near Somerset West, *Ecklon & Zeyher Irid. 294* (83) (B, FI, G, MO, S); Hottentots Holland, *Zeyher 391* (B), *Hutchinson 473* (K, PRE); slope above road to Disa Kloof, Bettys Bay (BD), *Ebersohn 270* (NBG); Groot Hangklip, *Boucher 585* (PRE, STE); near Oudebos, Palmiet River valley, *Boucher 1889* (STE).

3419 (Caledon) Top of Houw Hoek Pass (AA), *Goldblatt 371* (BOL); 6 mi. N of Bot Rivier, *Goldblatt 217* (BOL); Lebanon Forest Reserve, Catchment II, *Kruger 584* (NBG); Vijoens Pass, *Stokoe s.n.* (SAM 49613), *Strey s.n.* (M); Caledon commonage (AB), *Guthrie s.n.* (BOL); hillside near Caledon, *Crocker s.n.* (J 19879); Drayton siding, E of Caledon, *Goldblatt 341* (BOL); Zwartberg, Caledon, *Zeyher 3959* (BOL); clay slopes W of Eseljag Pass near Witdraai, *Goldblatt 4019* (MO); Highlands (AC), *Leighton 282* (BOL), *Compton 13478* (NBG); Hermanus, *Salter 1184* (BM), *Oldridge s.n.* (BOL); prope Hermanuspietersfontein, *H. Bolus 9845* (Z); Fern Kloof Nature Reserve, Hermanus, *Orchard 197* (MO, STE), *565* (MO), *Goldblatt 5177* (MO), *Woodvine 75* (MO, STE); Shaws Mountain (AD), *Barker 11* (BOL, K), Vogelklip, Hermanus, *Barker 1795* (NBG), *Goldblatt 7033* (MO); Hemel en Aarde, top of pass, *Gillett 1055* (STE); Mt. slopes behind Mossel River, *Martin 564* (NBG); Klein River Mts., *Stokoe s.n.* (SAM 55713, 59841); "Kleynriviersberg," *Ecklon & Zeyher Irid. 219* (58.8) (BM); Kleinriviersberge, *Zeyher 3959, 3959a* (B, BM, G, K, P, SAM, W, Z); Stanford valley, *Engler s.n.* (B); 26 mi. W of Riviersonderend (BA), *Mauve 4705* (PRE); Fairfield (BC), *Thomas s.n.* (NBG 60659); between Baardscheerdersbos and Pearly Beach (DA), *Mathews 2* (NBG, STE);

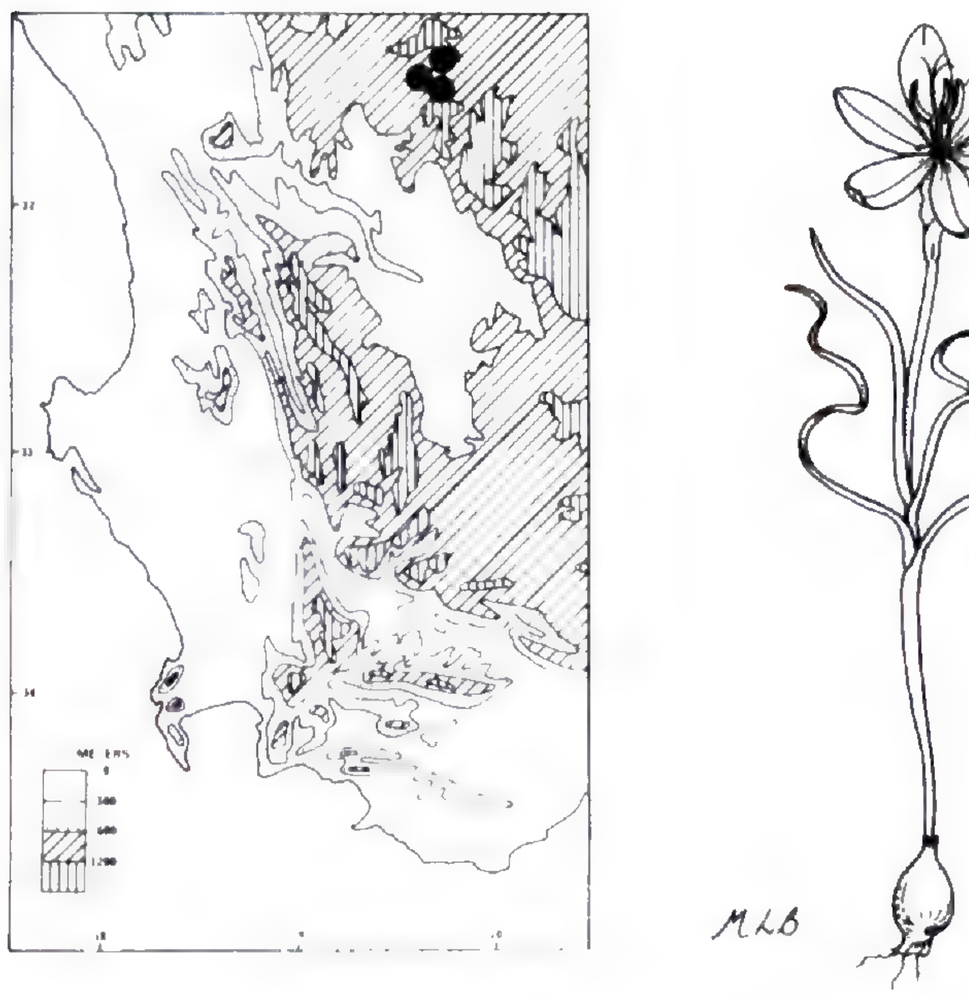


FIGURE 33. Morphology and distribution of *Geissorhiza corrugata*. Plant life size (*Goldblatt 3985*, flats S of Calvinia).

road to Ratel River, Bredasdorp, *van Niekerk 304* (NBG).

3420 (Bredasdorp) road to Bontebok Park, 1 mi. S of main highway (AB), *Goldblatt 3723* (MO, PRE, WAG); Bontebok Park, *Liebenberg 6453* (PRE), *Grobler 401* (STE); near Slang River, base of the Langeberg (BB), *Muir 5018* (NBG).

WITHOUT PRECISE LOCALITY: Capstadt, *Spielhaus s.n.* (B); Cape, *Bergius s.n.* (B, G), *Mund s.n.* (B), *Siebold 549* (B), *Drège 1556* (B), *Lichtenstein s.n.* (B), *Niven s.n.* (BR), *Thunberg s.n.* (S "Herb. Castrom," "Herb. Montin," "Herb. Swartz," UPS), *Pappe s.n.* (S), *Masson s.n.* (BM), *Roxburgh s.n.* (BM, G), *Alexander s.n.* (1847) (K), *Bowie s.n.* (1817) (BM).

SECTION *TORTUOSA*

2. Section **Tortuosa** Foster, Contr. Gray Herb. 135: 69. 1941. TYPE: *G. corrugata* Klatt.

Leaves linear to subterete, all basal, straight or twisted, *stem* smooth, short, 1-flowered, *bracts* herbaceous, *flowers* actinomorphic or declinate (*G. karooica*), the *style* shorter than or reaching to the apex of the *anthers*.

19. Geissorhiza corrugata Klatt, Abh. Naturf. Ges. Halle 12: 391 (Erg. 57). 1882. TYPE: South Africa. Cape: Hantam-Gebirge, *Meyer 24* (holotype, B). FIGURES 2, 33.

Plants small, to 5 cm high including flowers. *Corm* asymmetric, ovoid with an oblique flat side extending downward as a prominent ridge, 5–7 mm diam., tunics brown, concentric. *Cataphyll* single, membranous. *Leaves* 3–4, all basal, reaching the flowers, 1–2 mm wide, spirally twisted, margins lightly thickened, the uppermost sheathing the stem below and more or less straight. *Stem* erect, single or 2–3 produced from the base. *Spike* 1(–2)-flowered; *bracts* 12–15 mm long, membranous, spreading above, pale, or flushed red above, the inner slightly shorter than the outer. *Flowers* yellow, campanulate; *perianth tube* to 3 mm long, infundibuliform; *tepals* 12–15 mm long, ovate, outer 5–6 mm wide, inner 4–5 mm wide. *Filaments* 4–5 mm long; *anthers* 5 mm long, yellow. *Ovary* 2–4 mm long, *style* 6–7 mm, dividing near the base of the anthers, branches to 6 mm long, spreading to laxly recurved. *Capsule* globose to ovoid, 8–10 mm long. *Chromosome number*, $2n = 26$ (*Goldblatt 3895*).

Flowering time. August to September.

Distribution. Shale flats in the Calvinia district of the western Karoo. Figure 33.

Geissorhiza corrugata is a distinctive species, unusual in its spirally coiled leaves, solitary flowered inflorescences and style which branches towards the base instead of the apex of the anthers as is typical of most species of *Geissorhiza*. It shares these characters with the closely related, purple-flowered *G. spiralis*, from which it differs in having bright yellow flowers and a shorter perianth tube. Both species occur in the western Karoo (Figs. 33, 34), *G. corrugata* in the north, in the Calvinia district, and *G. spiralis* to the south in the southern Roggeveld around Sutherland.

The style of *Geissorhiza corrugata* and *G. spiralis* is intermediate between that found in *Geissorhiza* itself and in the related *Hesperantha*. In *Geissorhiza*, the style usually divides above the anthers, and the branches are typically short and recurved, while in *Hesperantha* the style divides at the top of a cylindric perianth tube (rarely within the tube) and the branches are long and spreading. Despite this intermediate type of style, the two species in question do not seem in any way connected with *Hesperantha*. *Geissorhiza corrugata* is self-compatible and autogamous, at least in the greenhouse, and its short style may be an adaptation to self-fertilization, the style branches being in contact with pollen during flowering. Reproductive biology is not known for *G. spiralis* but it may well be similar.

Specimens examined. SOUTH AFRICA. CAPE: 3119 (Calvinia) Hantam-Gebirge (BD), *Meyer 24* (B); marshy ground near Calvinia, *Schmidt 323* (PRE); 19 km S of Calvinia on Ceres Road, shale flats (DA), *Goldblatt 3985* (E, K, MO, NBG, PRE, S, US, WAG), *6257* (BR,

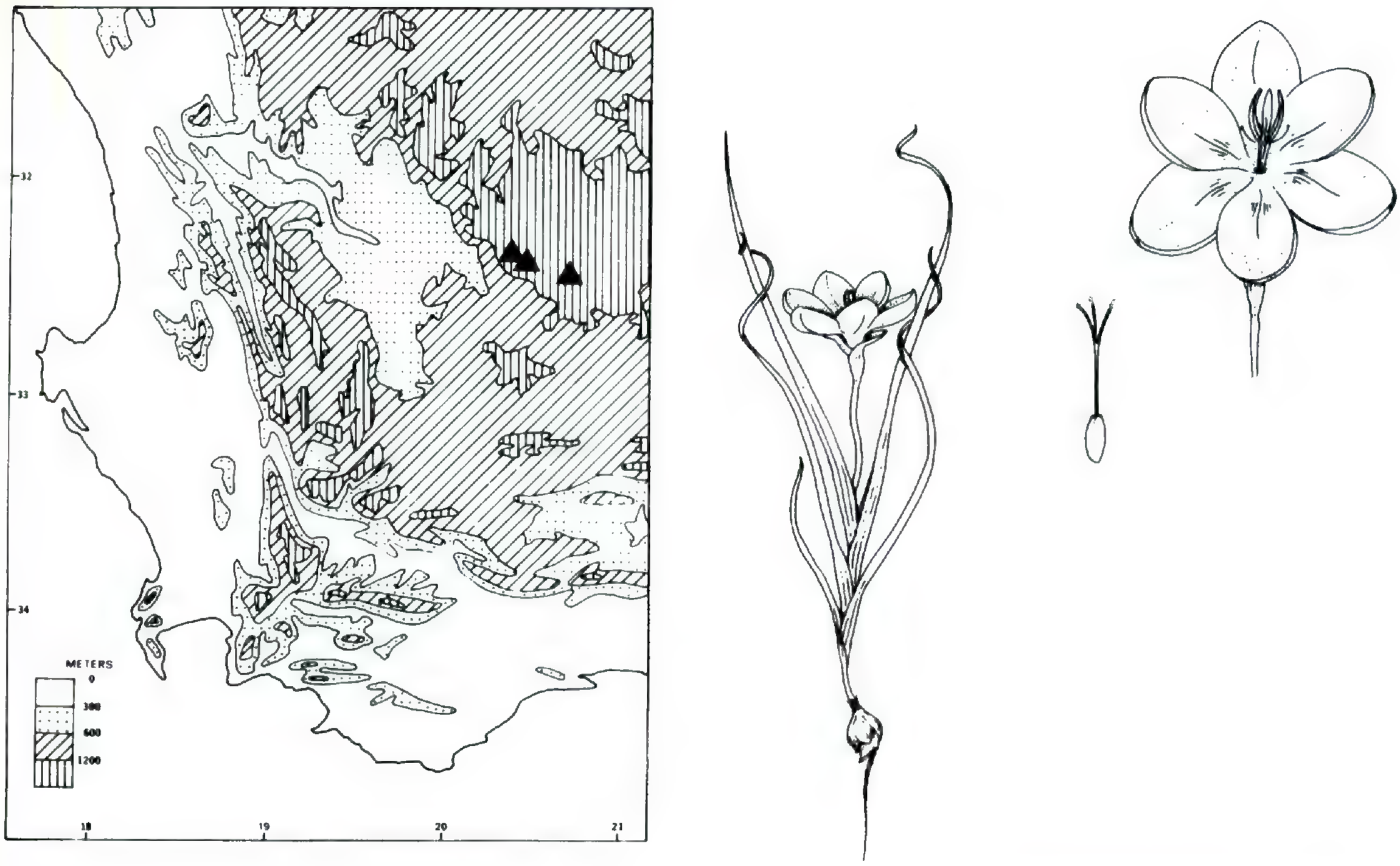


FIGURE 34. Morphology and distribution of *Geissorhiza spiralis*. Habit ×0.5; flower and gynoecium life size (*Lavranos 20617*, NE of Sutherland).

C, MO, NU); Karigabosch Fontein, flats S of Calvinia, *Thompson 2455* (STE); 5 mi. SSE of Calvinia (DB), *Acocks 18940* (PRE, STE).

DOUBTFUL LOCALITY: Truders Pass, Namaqualand, *Stayner s.n.* (NBG 87605).

20. Geissorhiza spiralis (Burchell) De Vos ex Goldbl., comb. nov. *Trichonema spiralis* Burchell, Trav. S. Africa 1: 260. 1822. *Geissorhiza spiralis* (Burchell) De Vos, J. S. African Bot. Suppl. 9: 295. 1973, comb. inval. basion. et lit. ref. non cit. *Romulea spiralis* (Burchell) Baker, J. Linn. Soc., Bot. 16: 90. 1878. TYPE: South Africa. Cape: Roggeveld, Jakhalsfontein-Renosterrivier, *Burchell 1356* (holotype, K). FIGURE 34.

Plants 2.5–4.5 cm high, including the flowers. *Corm* asymmetric, ovoid with an oblique flat side below, extending downward shortly, 4–7 mm diam., tunics brown, concentric. *Cataphyll* solitary, membranous. *Leaves* usually 4, basal, coiled or twisted distally, the uppermost sometimes straight and usually sheathing part or all of the stem, 0.5–2 mm wide, with the margins and midrib lightly thickened. *Stem* single, or 2–3 produced from the base, partly or entirely concealed by leaf bases. *Spikes* solitary flowered; *bracts* 10–13 mm long, membranous, purple-flushed, the inner bracts slightly shorter than the outer. *Flower* broadly campanulate, purple, with darker marks towards the base of the tepals, the tepal bases and tube pale yellow; *perianth tube* 4–5 mm long, infundibuliform; *tepals* 13–15 mm long, broadly ovate, outer to 10 mm wide, inner to 8 mm wide. *Filaments* 4 mm long; *anthers* 5–6 mm long. *Ovary* ca. 3 mm long but enlarging rapidly after fertilization, *style* 6–7 mm long, dividing near the base of the anthers; *branches* 5 mm long, laxly spreading, not recurved. *Capsule* unknown. *Chromosome number*, unknown.

Flowering time. September.

Distribution. Known only from the southern Roggeveld near and to the east of Sutherland. Figure 34.

Geissorhiza spiralis was discovered in the early nineteenth century by William Burchell, the famous traveller-explorer of southern Africa. Burchell (1822) described it in his "Travels in the Interior of Southern Africa," assigning it to the genus *Trichonema* (syn. *Romulea*). Its correct identity was only recently established by De Vos (1972) during her studies on *Romulea*. Her proposed combination in *Geissorhiza* is without ci-

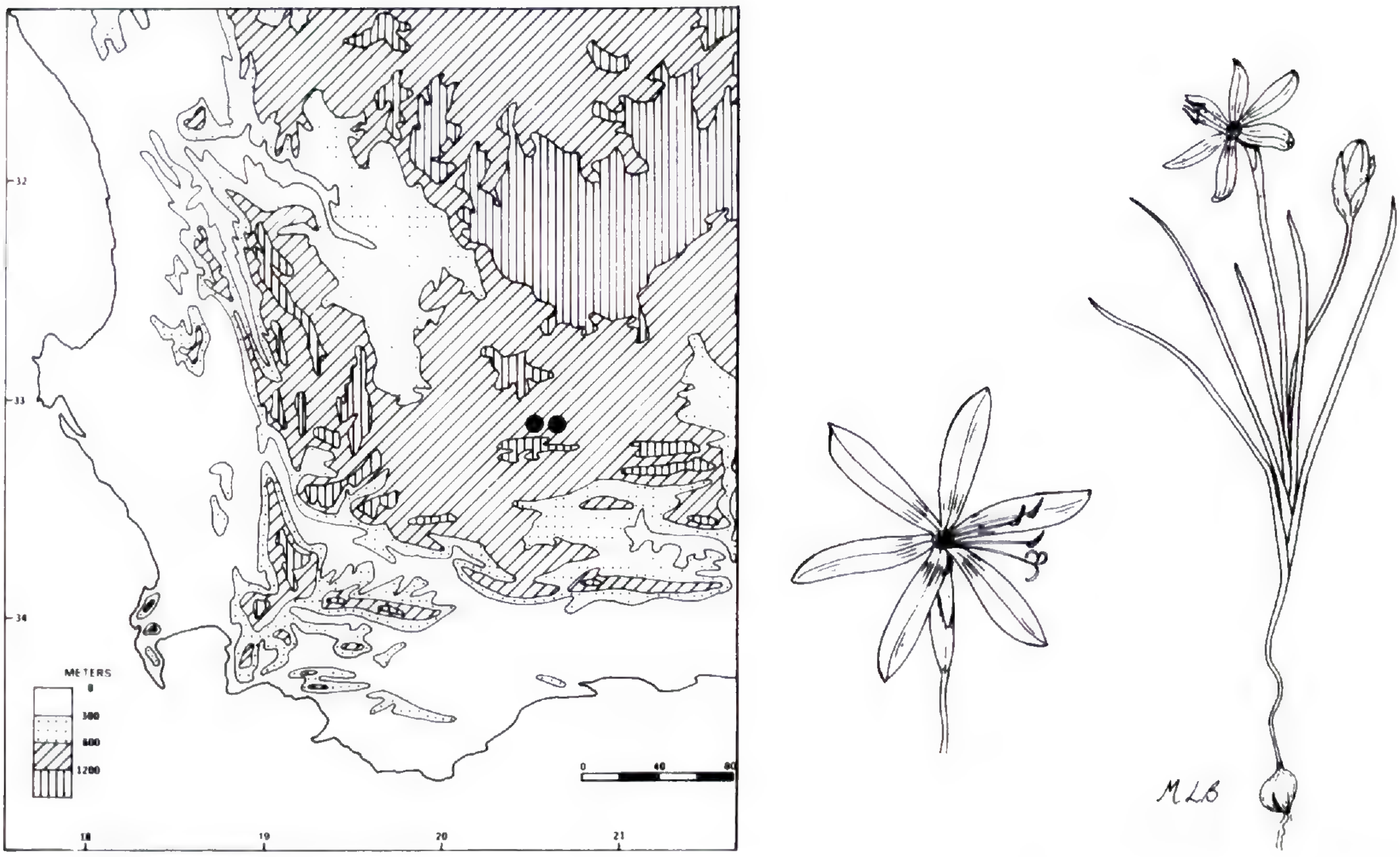


FIGURE 35. Morphology and distribution of *Geissorhiza karooica*. Habit ×0.5; flower life size (*Goldblatt 6371*, Ghaap Kop, Matjesfontein).

tation of the basionym and place of original publication and thus invalid. The necessary citations are included here for legitimate combination.

The species is unusual in its several twisted leaves, solitary flowered spikes and style dividing at the base of the anthers. These features are also found in *Geissorhiza corrugata*, to which it is undoubtedly related. *Geissorhiza spiralis* can be distinguished from *Geissorhiza corrugata* by its purple flowers with a perianth tube 4–5 mm long as compared to the yellow flowers and short perianth tube, ca. 3 mm long of *G. corrugata*.

Specimens examined. SOUTH AFRICA. CAPE: 3220 (Sutherland) 30 km NE of Sutherland (BB), *Lavranos 20617* (NBG); stony vlakte near Sutherland (BC), *Joubert & De Vos 1584* (SAM, STE); SW of Sutherland, *De Vos 2260* (STE); stony plain towards Waterkloof; *Marloth 10404* (PRE, STE); Jakalsfontein-Renosterrivier (?BD), *Burchell 1356* (K).

21. Geissorhiza karooica Goldbl., sp. nov. TYPE: South Africa. Cape: near Matjesfontein, foot of Ghaap Kop, *Goldblatt 6371* (holotype, MO; isotypes, BOL, K, NBG, PRE, S, UC, US, WAG). FIGURES 3, 35.

Planta 3–6 cm alta, foliis 4–6 basalibus erectis vel falcatis linearibus, spica florum unum, floribus hypocrateriformibus declinatis atrocaeruleis luteis in fauce, tubo (5–)6–8 mm longo, tepalis 12–15 mm longis, antheris 2.5–3.3 mm longis, stylo diviso prope basem antherarum, ramis recurvatis.

Plants 3–6 cm high. *Corm* globose, ca. 5 mm diam., tunics light brown, concentric, the outer layers breaking vertically into unequal sections. *Cataphyll* pale, dry, membranous. *Leaves* 4–6, linear, 1–1.8 mm wide, about as long as the stem, all basal, the upper 2–3 sheathing the stem below, erect, or becoming falcate, blade plane, margins not thickened. *Stems* 1–4, produced from the base. *Spike* solitary flowered; *bracts* 8–12 mm long, dry and membranous, brown above, reddish below, the inner about as long or slightly shorter than the outer. *Flowers* hypocrateriform, zygomorphic, dark violet purple, yellow at the base of the tepals and in the throat; *perianth tube* (5–)6–8 mm long, nearly cylindric, exserted from the bracts; *tepals* subequal, lanceolate, obtuse, 12–15 mm long, to 4–5 mm wide, extending at right angles to tube when fully open. *Filaments* 8–10 mm long, unilateral and declinate; *anthers* 2.5–3.3 mm long, pollen yellow. *Ovary* ca. 4 mm long, *style* dividing between the base and midline

of the anthers, branches 1.2–2 mm long, recurved. *Capsule* oblong to globose, 8–11 mm long. *Chromosome number,* $2n = 26$ (*Goldblatt 6371*).

Flowering time. August to September.

Distribution. Margins of the western Karoo, north of the Witteberg, between Matjesfontein and Whitehill, on coarse shaley slopes. Figure 35.

This distinctive, dwarf species of *Geissorhiza* has so far been found in only two localities, in the arid southwestern Karoo north of the Witteberg Mountains in the Laingsburg district. It is unusual in having flowers solitary on the stems, of which up to four may be produced on each plant. The bright violet purple flowers are large and attractive and unusual in being zygomorphic. The stamens are unilateral and declinate while the tepals are subequal and regularly disposed. The four to six leaves are all inserted at the base, and are narrow and linear, but otherwise unremarkable.

Geissorhiza karooica appears to be allied to two peculiar species of the western Karoo, *G. spiralis* and *G. corrugata,* which have similar but actinomorphic flowers borne singly on each stalk, but have spirally coiled leaves and are also distinctive in having the style dividing near the anther base, a feature unusual in the genus. It seems likely that *G. karooica* is close to the line which gave rise to these two very reduced and unusual species of *Geissorhiza,* and the three species are united here in section *Tortuosa* of subgenus *Weihea.*

Specimens examined. SOUTH AFRICA. CAPE: 3320 (Montagu) Whitehill, Laingsburg (BA), *L. Bolus s.n.* (BOL 19156); base of Ngaap Kop, near Matjesfontein, *Esterhuysen 32639* (BOL, MO); shaley flats W of Ngaap Kop, *Oliver 3488* (STE); Ghaap Kop, abundant near base of shaley S-facing slope, *Goldblatt 6371* (BOL, K, MO, NBG, PRE, S, UC, US, WAG).

SECTION *PUSILLA*

3. Section **Pusilla** Goldbl., sect. nov. TYPE: *G. pusilla* (Andr.) Klatt.

Tunicae cormi lignosae, foliis planis infra et in marginibus pubescentibus, caule glabro, spica pauciflora, bracteis infra herbaceis supra siccis ferrugineis, floribus stellatis, tubo brevi.

Corm tunics woody, *leaves* ensiform, plane, pubescent on the margins and on the lower part of the blade, *stem* smooth, *spike* few flowered, *bracts* herbaceous below, dry and ferrugineous in the upper half, *flowers* stellate, tube very short.

Species. 1.

22. Geissorhiza pusilla (Andr.) Klatt, Abh. Naturf. Ges. Halle (Erg. 58). 1882; Foster, Contr. Gray Herb. 135: 50–51. 1941. *Ixia pusilla* Andr., Bot. Repos. 4: tab. 245. 1802. *Geissorhiza secunda* var. *pusilla* (Andr.) Baker, Handb. Irid. 155. 1892, Fl. Cap. 6: 69. 1896. TYPE: South Africa. Cape: exact locality unknown (figure in Andr., Bot. Repos. 4: tab. 245. 1802). FIGURE 36.

Ixia secunda Ker excl. fig. et descr., Bot. Mag. 17: tab. 597. 1802, hom. illeg. non de la Roche (1768) et nom. illeg. superfl. pro *Ixia pusilla* Andr.

Geissorhiza secunda Ker, nonsensu Ker, Ann. Bot., (König & Sims) 1: 225. 1804, nom. illeg. superfl. (name applied to *G. aspera*).

Geissorhiza pubescens Wolley Dod, J. Bot. 38: 171. 1900. TYPE: South Africa. Cape: Signal Hill, *Wolley Dod 1602* [lectotype K, effectively designated by Foster (1941: 50); isolectotypes, B, BM, BOL]; Signal Hill, W slopes, *Wolley Dod 1246* (syntype, BOL).

Geissorhiza nigromontana Ecklon ms. (Zwarteberg bei Caledons Bad.)

Plants small to medium, 7–30 cm high. *Corm* 4–10 mm diam., globose, evidently asymmetric with a down-pointing projection on one side, tunics light brown, concentric. *Cataphyll* solitary, membranous, reaching ground level. *Leaves* 2–4, the lower, or all basal, the second or third leaf usually sheathing stem for about half its length, ensiform, erect to falcate, the longest not reaching the base of the spike, 3–8 mm wide, margins and sometimes lower part of the blade or sheath pubescent with long hairs, the margins also often ciliate, the uppermost leaf short, sometimes bract-like. *Stem* smooth, erect, simple or 1–2-branched. *Spike* (1–)2–6-flowered; *bracts* herbaceous below, brown and dry in the upper half and spreading, 5–8 mm long, the inner smaller than the outer. *Flower* stellate, pale to deep blue or blue-mauve; *perianth tube* 1–2 mm long, infundibuliform; *tepals* 7–10 mm long, to 4 mm wide. *Filaments* 2 mm long; *anthers* to 3 mm long, yellow. *Ovary* ca. 2 mm long, *style* 4–5 mm long, the branches ca. 1 mm long, recurved. *Capsule* obovoid to sub-globose, 5–7 mm long. *Chromosome number,* $2n = 26$ (*Goldblatt 196*).

Flowering time. (Late August to) September to early October.

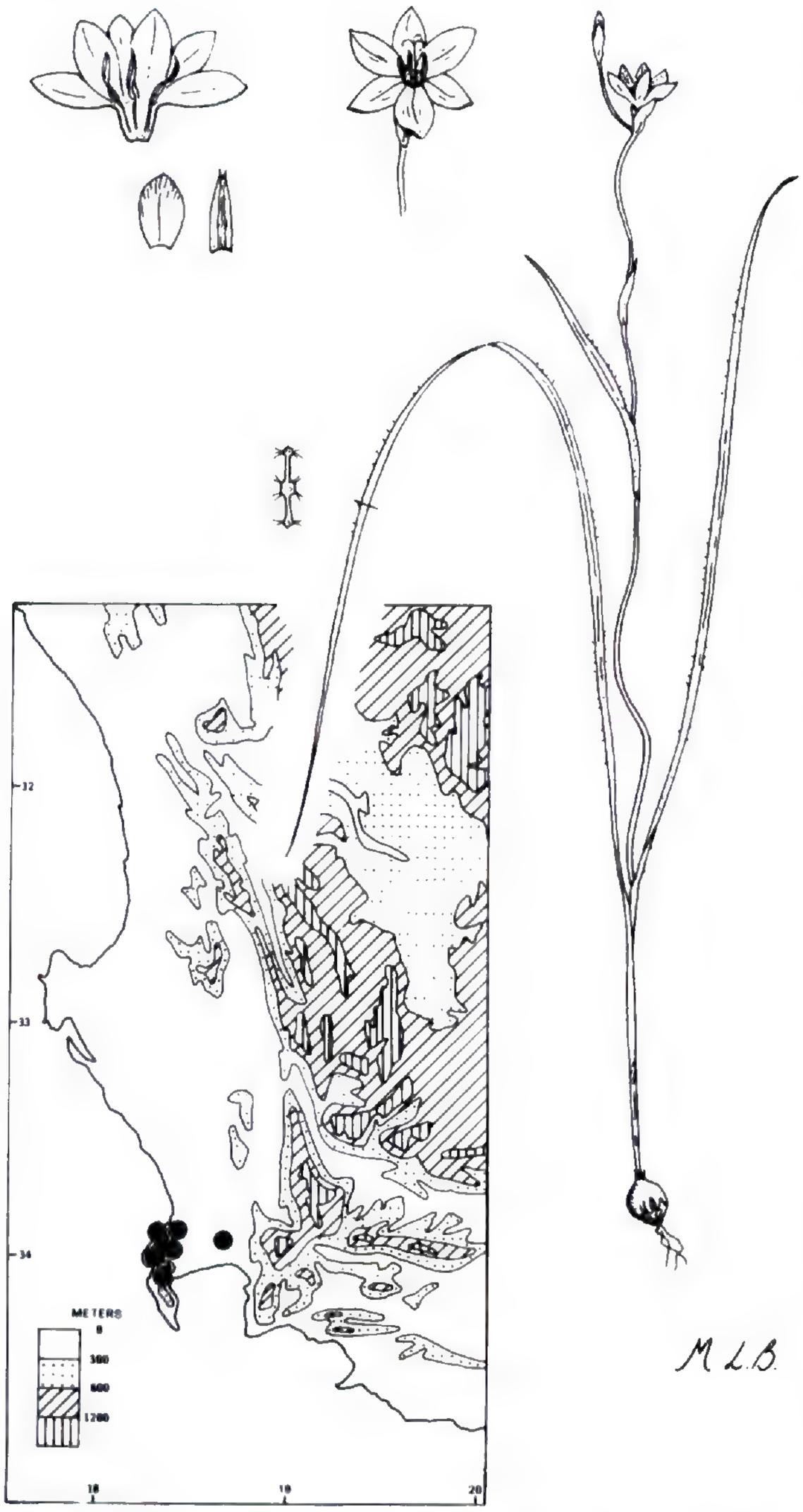


FIGURE 36. Morphology and distribution of *Geissorhiza pusilla*. Habit ×0.5; flowers and separated bracts life size; leaf section much enlarged (*Goldblatt 6643*, Contour path, Kirstenbosch).

Distribution. Damp, often shady situations, mainly montane at low to middle elevations, Cape Peninsula and nearby hills. Figure 36.

As Wolley Dod correctly observed when describing *Geissorhiza pubescens*, a later synonym of *G. pusilla*, it closely resembles the very common *G. aspera* (syn. *G. secunda* sensu auct.) in general appearance, but is in fact quite distinct. It has light brown concentric corm tunics, typical of subgenus *Weihea*, and it must be assigned to this subgenus. The leaves are pubescent, the stem smooth, and the flower is rather smaller and paler than is typical of *G. aspera*. *Geissorhiza pusilla* appears to have no close allies, and its relationships within subgenus *Weihea* are obscure. It may have an intersectional hybrid origin between species of section *Weihea* and either section *Ciliata* or *Planifolia* of subgenus *Geissorhiza*.

The type material of *Geissorhiza pusilla* is, as far as is known, the colored illustration in Andrews (Bot. Rep. 4: tab. 245. 1802). As Foster (1941) observes, the critical features of the species are not illustrated clearly. The corm tunics are merely shown as uniform light brown and there is no hint of the very characteristic leaf pubescence. Nevertheless, the aspect of the plant, its small, pale blue flower and corm color make it seem very likely that the interpretation placed on it by Klatt (1882) and Foster (1941) is correct.

Geissorhiza pusilla is relatively uncommon and it is found only in damper situations, mainly on heavier soils. It is restricted to the Cape Peninsula and the surrounding hills.

Specimens examined. SOUTH AFRICA. CAPE: 3318 (Cape Town) Cape Peninsula, slopes of Lions Head (CD), *Lewis 1077* (SAM), *Salter 7630* (SAM), *Schlechter 1360* (B, Z), *Barker 3866* (NBG), *Ecklon s.n.* (S); Signal Hill, *Penfold s.n.* (SAM 52895), *Wolley Dod 1246* (BOL), *1602* (B, BM, BOL, K), *Barker 407* (NBG), *Goldblatt 196* (BOL); near Zonnebloem, slopes of Table Mt., *MacOwan 2270* (K, SAM), *Zeyher 81* (K, SAM); Devils Mt., opposite Woodstock, *Scott Elliot 1078* (E); Devils Peak, above Groot Schuur, *Wolley Dod 583* (BM, BOL); slopes of Devils Peak near Prince of Wales Blockhouse, *Goldblatt 2719* (MO, PRE, US); foot of Devils Peak, *Pappe s.n.* (BM); contour path above Kirstenbosch between Skeleton and Window gorge, *Goldblatt 4832* (MO); Kirstenbosch, Castle Buttress above the contour path, *Goldblatt 6643* (MO); Langverwacht, above Kuils Rivier (flowers opening mornings only) (DC), *Oliver 4697* (K, MO, PRE).

3319 (Simonstown) Hout Bay (AB), *Bond 1224* (NBG); Noordhoek, *Dame Alice & the Misses Godman 313* (BM).

WITHOUT PRECISE LOCALITY: Cape of Good Hope (C.B.S.), *Lalande s.n.* (B); Capstatt, *Spilhaus s.n.* (B "Herb. Lubeck"), *Verreaux s.n.* (G), *Mund s.n.* (K).

DOUBTFUL LOCALITY: Caledon Zwartberg at the Baths, *Ecklon s.n.* (S); Hex River Valley, *Dame Alice & the Misses Godman 487* (BM).

SECTION *INCLUDANTHERA*

4. Section **Includanthera** Goldbl., sect. nov. TYPE: *G. cedarmontana* Goldbl.

Tunicae cormi lignosae, foliis linearibus planis vel marginibus costisque incrassatis, spica pauciflora, floribus hypocrateriformibus, tubo longo e bracteis exsertis, staminibus styloque in tubo inclusis.

Corm tunics woody, *leaves* linear, plane or with the margins and midrib thickened, *spike* few flowered, *flowers* hypocrateriform, tube long, exserted from the bracts, the stamens and style very short and included in the lower half of the tube.

The two species of the section do not have the characteristic well-exserted style and stamens of *Geissorhiza*. The included stamens and style are clearly a secondary development and derived. In leaf, corm (not known for *G. esterhuyseniae*), and bract morphology, however, they accord well with *Geissorhiza* subgenus *Weihea*. Moreover, the style branches are short and thus consistent with the genus.

Species. 2.

23. Geissorhiza esterhuyseniae Goldbl., sp. nov. TYPE: South Africa. Cape: Great Winterhoek, crevices in cliffs and rocky ledges, *Esterhuysen 28519A* (holotype, BOL).

Planta 7–18 cm alta, foliis (2–)3 lineari-falcatis, caule prostrato, floribus albis, hypocrateriformibus, tubo perianthii 10–16 mm longo, staminibus styloque inclusis, filamentis 3 mm longis, antheris 4.5 mm longis, stylo 0.5 mm longo, ramis ca. 2 mm longis, divergentibus.

Plants 7–18 cm high. *Corms* unknown. *Cataphyll* dry, membranous, brown below. *Leaves* (2–)3, plane, all basal or the uppermost inserted in lower part of stem, sometimes bract-like, linear or falcate, 3–5 mm wide, about half as long as the stem, obtuse, the margins lightly thickened. *Stem* apparently declinate to trailing from steeply inclined surfaces, smooth, bearing a sheathing bract in upper part. *Spike* 1–3-flowered; *bracts* 12–14 mm long, green, becoming pale and membranous above, the inner bracts about as long, or shorter than the outer. *Flower* hypocrateriform, white, fragrant; *perianth tube* cylindric, 10–16 mm long, including the stamens and style, well-exserted from the bracts; *tepals* obovate 13–15 mm long, ? ca. 7 mm wide. *Filaments* ca. 3 mm long, inserted 2.5 mm from the base of the tube; *anthers* included in the perianth tube, 4.5 mm long, not reaching the middle part of the tube. *Ovary* 3–4 mm long, *style* short, 0.5 mm long, branches ca. 2 mm, diverging. *Capsule* and *seeds* unknown. *Chromosome number,* unknown.

Flowering time. October.

Distribution. Known only from a single collection from high altitudes in the Great Winterhoek Mountains. Figure 37.

Geissorhiza esterhuyseniae is known only from a single gathering made by Elsie Esterhuysen, the well known Cape botanist, after whom the species is named. Her extensive collecting has made an extraordinary contribution to the knowledge of the Cape Flora, especially of mountain areas. This species is one of the most remarkable in the genus, having both stamens and style included within a long perianth tube. This set of characters is known in *Geissorhiza* elsewhere only in the northern Cedarberg species, *G. cedarmontana,* and these two species stand well apart in the genus. Differences and similarities between *G. esterhuyseniae* and *G. cedarmontana* are discussed fully under *G. cedarmontana,* the following species in this treatment. As the corms of *G. esterhuyseniae* are unknown, it is not possible to place the species to subgenus with certainty but in the absence of data to the contrary, *G. esterhuyseniae* is assumed to be related to *G. cedarmontana* and is assigned subgenus *Weihea* section *Includanthera.*

Both species grow at high altitudes in the mountains that run parallel to the western Cape coast, and in similar habitats, sheltered south-facing rocky situations. *Geissorhiza esterhuyseniae* occurs in the Great Winterhoek mountains at 2,000 m and *G. cedarmontana* in the northern Cedarberg, some 80 km to the north at altitudes above 1,200 m. It is likely that more localities for both will be found when the higher mountains separating the known ranges of the two species are more fully explored botanically.

It is interesting to point out that the unusual suite of floral characters found in *Geissorhiza esterhuyseniae* and *G. cedarmontana* also occur in two taxonomically isolated species of the related genus *Hesperantha, H. elsiae* and *H. cedarmontana,* as well as in *Ixia paniculata,* all of which also grow in the western part of the Cape Floristic Region. In the *Hesperantha* species, the style branches themselves are long as is typical for this genus, and the *Ixia* species has short style branches and corms with the reticulate tunics characteristic of *Ixia.*

Specimen examined. SOUTH AFRICA. CAPE: 3319 (Worcester) Great Winterhoek, 6,000 ft., cliffs and rock ledges, south aspect (AA), *Esterhuysen 28519A* (BOL).

24. Geissorhiza cedarmontana Goldbl., sp. nov. TYPE: South Africa. Cape: Cedarberg, Mid-

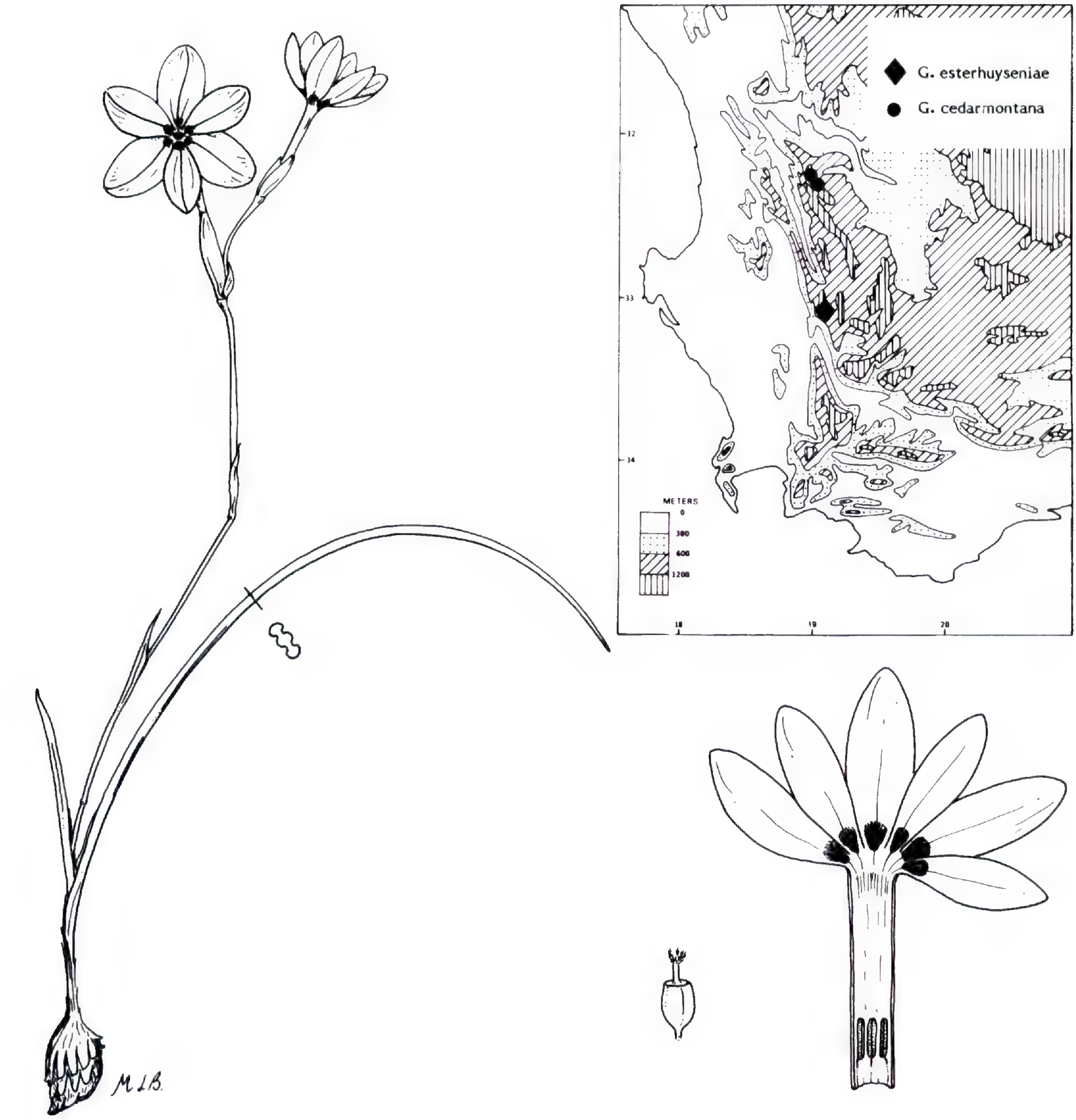


FIGURE 37. Morphology and distribution of *Geissorhiza cedarmontana* and distribution of *G. esterhuyseniae*. Habit life size; opened flower and gynoecium ×2; leaf section enlarged (*Goldblatt 5145*, Middelberg, Cedarberg).

delberg, *Goldblatt 5145* (holotype, MO; isotypes, K, NBG, PRE, S, WAG). FIGURES 4, 37.

Planta (7–)12–35 cm alta, cormo symmetrico, tunicis concentricis, foliis 2(–3), linearibus, caule erecto vel inclinato, spica (1–)2–5 florum, floribus hypocrateriformibus subroseis, maculis rubris ad basem tepalorum, tubo perianthii 13–15 mm longo, staminibus styloque inclusis, filamentis ca. 1 mm longis, antheris ca. 3 mm longis, stylo ca. 1 mm longo, ramis brevibus.

Plants (7–)12–35 cm high. *Corm* globose, symmetric, ca. 10 mm diam., tunics concentric, pale brown, notched below into segments and drawn into bristles above. *Cataphyll* membranous, brownish. *Leaves* 2–3, usually the lower two well-developed and basal, the upper of these sheathing the stem for some distance, linear, shorter or about as long as the stem, ca. 1.5 mm wide, margins and midrib heavily thickened, leaving 2 longitudinal grooves running along each leaf

surface, the uppermost leaf cauline, sometimes reduced and bract-like. *Stem* erect or inclined, bearing a cauline leaf below, and often bearing 1(–2) green to membranous sheathing bract-leaves, unbranched. *Spike* flexuose (1–)2–5-flowered; *bracts* 7–11 mm long, herbaceous, with hyaline margin, the outer obtuse, the inner membranous, slightly shorter than the outer. *Flowers* hypocrateriform, pale to deep pink, with a red mark at the base of each tepal; *perianth tube* cylindric, 13–15 mm long, well-exserted, including the stamens and style; *tepals* 12–14 mm long, ovoid, spreading, outer up to 7 mm wide, inner 6 mm wide. *Filaments* ca. 1 mm long, inserted 1.5–2 mm above the base of the perianth tube; *anthers* ca. 3 mm long, included in the tube, and not extending beyond the middle of the tube. Ovary 2–3 mm long, *style* very short, less than 1 mm long with 3 short branches. *Capsule* obovoid, 5–6 mm long; *seeds* angular. *Chromosome number*, $2n = 26$ (*Goldblatt 5145*).

Flowering time. Mid-October to November.

Distribution. Cedarberg, high altitudes on south-facing slopes, in rock seams or under boulders. Figure 37.

Geissorhiza cedarmontana and its less well known ally *G. esterhuyseniae* are unique in the genus in having both stamens and style branches entirely included within the long perianth tube. They appear to be quite isolated in subgenus *Weihea,* with no close allies and have been assigned to a separate section, *Includanthera.* Of the two species, *Geissorhiza cedarmontana* seems the more specialized, having very short filaments, ca. 1 mm long, inserted about 2 mm above the base of the perianth tube and a style less than 1 mm long, with three short poorly defined branches. The leaves are also modified, having much thickened margins and midrib, so that two longitudinal grooves run the length of each leaf surface. By contrast, *G. esterhuyseniae* has filaments about 3 mm long, inserted ca. 2.5 mm above the base of the perianth tube, and better developed style branches some 2 mm long. The leaves of *G. esterhuyseniae* are flat, with unthickened margins and midrib.

Both species occupy a similar habitat, growing at high altitudes, above 1,200 m, in sheltered south facing slopes and cliffs, often in cracks in rock faces, or under overhangs, where water is available for longer periods than in open areas. *Geissorhiza cedarmontana* blooms unusually late in the season, late spring to early summer, long after the last winter rains have fallen in the comparatively dry Cedarberg Mountains. It is known from a rather restricted area of the Cedarberg, in the Middelberg above Algeria, which is much frequented by hikers, but is quite likely more widespread, occurring in places seldom visited.

The character of included stamens and styles found in *Geissorhiza cedarmontana* and *G. esterhuyseniae* occurs in two species of the related genus *Hesperantha, H. elsiae* and *H. cedarmontana* and in *Ixia paniculata.* These species are also found in montane or occasionally lowland habitats in the western Cape mountains. It seems likely that their shared floral characters are an adaptation to some specialized pollinator, as yet unidentified.

Specimens examined. SOUTH AFRICA. CAPE: 3219 (Wuppertal) Cedarberg (AC), *Jackson s.n.* (SAM 68438); Middelberg, ca. 5,000 ft., *Jackson s.n.* (NBG 60731); S facing slopes of Middelberg Central, in seams in rock, *Goldblatt 5145* (K, MO, NBG, PRE, S, WAG); moist ledges near summit, Cedarberg above Algeria, *Galpin 10560* (PRE).

SECTION *ANGUSTIFOLIA*

5. Section **Angustifolia** Goldbl., sect. nov. TYPE: *G. humilis* (Thunb.) Ker.

Geissorhiza subsection *Filiformes* Foster, Contr. Gray Herb. 135: 18. 1941. TYPE: *G. juncea* (Link) A. Dietr.

Tunicae cormi durae lignosae, interdum molles, foliis 2–3, raro 1, ensiformibus vel linearibus et marginibus costisque incrassatis, vel teretibus, bracteis herbaceis vel membranaceis, saepe siccis supra, floribus actinomorphis, plerumque stellatis, tubo brevi, ad apicem bractearum extenso, vel longissimo.

Corm tunics hard and woody, occasionally soft in texture, *leaves* with the margins and midrib heavily thickened, ensiform to linear, sometimes terete, *bracts* herbaceous to membranous often dry above, *flowers* usually stellate, actinomorphic, the tube short, reaching to the apex of the bracts, or very long.

Species. 11.

25. Geissorhiza lithicola Goldbl., sp. nov. TYPE: South Africa. Cape: between Kogelberg and Steenbras, *Esterhuysen 35262* (holotype, BOL; isotypes, K, MO, PRE, S, WAG). FIGURE 38.

Planta 15–30 cm alta, tunicis cormi concentricis duris, foliis 3, inferioribus duobus linearibus quadrisulcatis, superiore infra vaginanti, caule erecto, spica 1–4 florum, floribus caeruleo-purpureis, tubo 7–8 mm

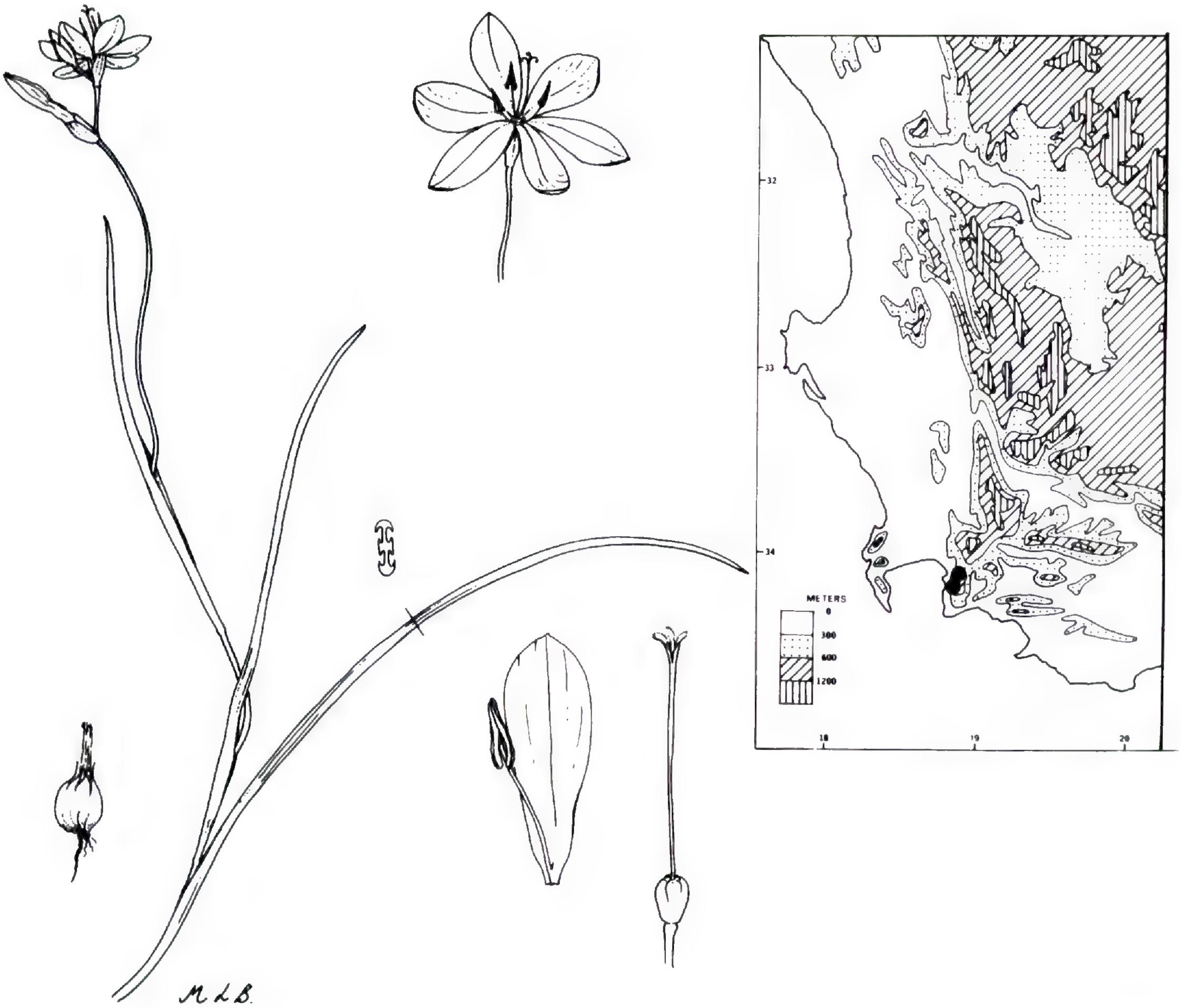


FIGURE 38. Morphology and distribution of *Geissorhiza lithicola*. Habit and corm ×0.5; flower life size; partial flower and gynoecium ×2 (*Esterhuysen 35262*, between Kogelberg and Steenbras Mts.).

longo, tepalis 15–20 mm longis, antheris ca. 5 mm longis.

Plants 15–30 cm high. *Corm* globose, flattened obliquely below, 6–10 mm diam., tunics concentric, light brown, woody, drawn into cusps above. *Cataphyll* membranous, decaying early, or not evident. *Leaves* 3 (rarely 2), linear, 1–2 mm wide, with 2 narrow grooves on each surface, the margins and midrib much thickened and minutely ciliate along their edges, the lowermost longest, basal, sticky in the lower half and densely covered with adhering sand, about half to as long as the stem, the middle leaf inserted at or near ground level, sheathing the lower part of the stem for a short distance, the uppermost leaf inserted in the mid part of the stem and partly sheathing below. *Stem* nearly erect, unbranched. *Spike* flexuose, 1–4-flowered; *bracts* 9–11 mm long, herbaceous below, becoming dry above, the inner shorter and narrower than the outer. *Flower* hypocrateriform, the tepals extended horizontally when fully open, purple to violet; *perianth tube* 7–8 mm long, reaching to about the apex of the bracts; *tepals* 15–20 mm long, oblanceolate, to 7–9 mm wide. *Filaments* 6–7 mm long; *anthers* ca. 5 mm long, pollen yellow. *Ovary* 2–3 mm long, *style* dividing near the apex of the anthers, becoming eccentric, branches 3–4 mm long, recurved. *Capsule* unknown. *Chromosome number,* unknown.

Flowering time. October.

Distribution. Middle altitudes in the Kogelberg Mountains. Figure 38.

Geissorhiza lithicola seems to be a link between sections *Angustifolia* and *Engysiphon* of subgenus *Weihea*. It has the hard, woody corm tunics characteristic of section *Engysiphon,* but

an actinomorphic, short-tubed flower, quite typical of section *Angustifolia*. Without the corms it is easily confused with *G. hesperanthoides* and *G. nubigena* of section *Ixiopsis*, both of which species have soft membranous to fibrous tunics. *Geissorhiza lithicola* can be distinguished from these two species by its more lightly thickened leaves, which have minutely ciliate edges. It also has a much shorter perianth tube than *G. nubigena* in which the tube is some 10–18 mm long and at anthesis well exserted from the bracts. The perianth tube of *G. hesperanthoides* is only 5–8 mm long at anthesis, extending to 7–10 mm in older flowers and typically not or barely exserted from the bracts, and confusion with this species is more likely. *Geissorhiza lithicola* is apparently restricted to the Kogelberg Mountains on the east side of False Bay, where it has only been collected twice, at low to middle elevations in very stony ground.

Specimens examined. SOUTH AFRICA. CAPE: 3418 (Simonstown) between Kogelberg and Steenbras (BB), *Esterhuysen 35262* (BOL, K, MO, PRE, S, WAG); Koeelbaai, *Loubser 959* (NBG).

26. Geissorhiza purpurascens Goldbl., sp. nov. TYPE: South Africa. Cape: Mamre road, *Barker 808* (holotype, NBG). FIGURE 39.

Planta (14–)18–30 cm alta, tunicis cormi concentricis, foliis 3, inferioribus duobus basalibus, linearibus marginibus costisque incrassatis quadricanaliculatis viscosis, superiore vaginanti infra vel omnino, caule erecto simplici vel 1-ramoso, spica 4–9 floribus, floribus stellatis, malvinis, tubo 3–4(–6) mm longo, tepalis 10–16 mm longis, antheris 3.5–4 mm longis, stylo diviso ad apicem antherarum, ramis recurvatis.

Plants (14–)18–30 cm high. *Corm* asymmetric, globose, with one side flattened below and produced downwards shortly, 6–8 mm diam., tunics concentric, pale brown, fragmenting irregularly and drawn into points above. *Cataphyll* membranous. *Leaves* 3 (or 2 if uppermost entirely sheathing and bract-like), the lower two basal, the lowermost longest, about half as long as the stem, sometimes longer, 2–3(–5) mm wide, sticky and with adhering sand, linear, margins and midrib thickened, broadly 2-channelled on each surface, the margins and the edges of the

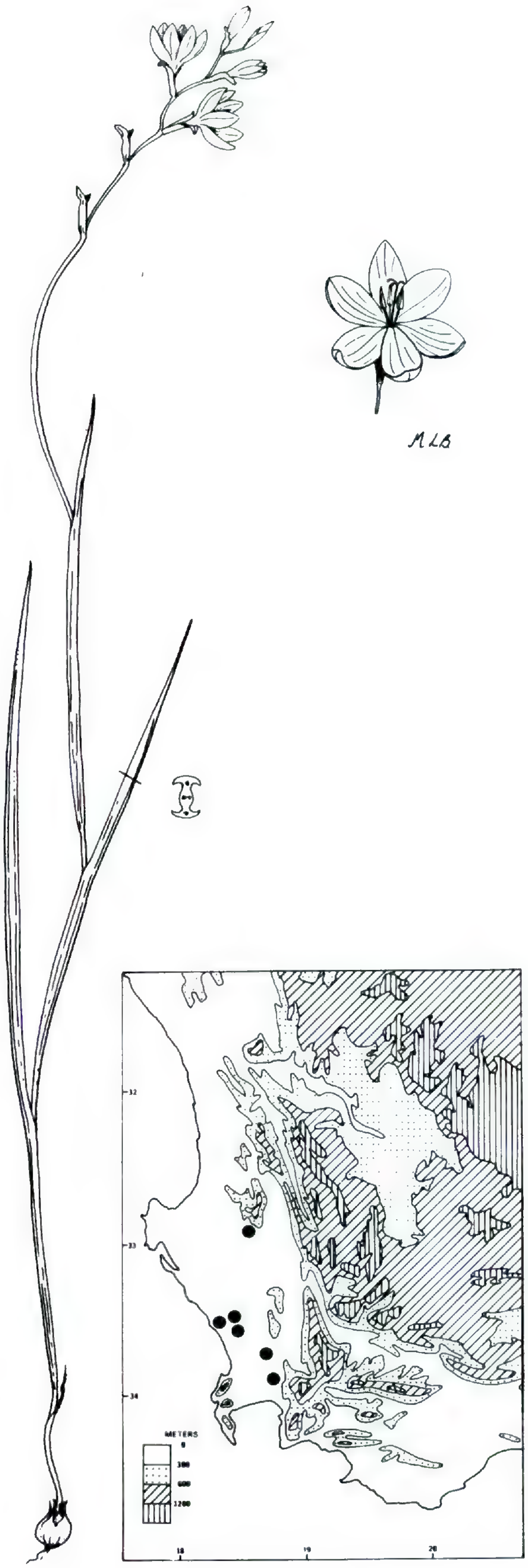


FIGURE 39. Morphology and distribution of *Geissorhiza purpurascens*. Habit ×0.5; flower life size; leaf section much enlarged (*Goldblatt s.n.*, Darling Flower Show, origin unknown).

midrib ciliate-pubescent, the second leaf similar but shorter and sheathing the stem below, the third leaf inserted in the middle part of the stem, partly to almost entirely sheathing. *Stem* erect, simple or with 1 branch, flexed above sheathing part of leaves. *Spike* 4–10-flowered, secund, drooping in bud, flexed at the base and flexuose; *bracts* 6–9 mm long, initially herbaceous with a hyaline margin, later dry and pale in upper half or entirely, the inner shorter than the outer. *Flower* stellate, pale mauve (darkening when dry); *perianth tube* 3–4(–6) mm long; *tepals* 10–16 mm long, 6–8 mm wide, elliptic. *Filaments* 4–6 mm long; *anthers* 3.5–4 mm long. *Ovary* 2 mm long, *style* dividing near the apex of the anthers, branches ca. 2.5 mm long, recurved. *Capsule* unknown. *Chromosome number,* unknown.

Flowering time. September to early October.

Distribution. Local on the west coast between Paarl Mountain and the coast at Mamre and Darling. Figure 39.

Geissorhiza purpurascens is a member of subgenus *Weihea,* and has the hard, concentric corm tunics typical of this group. It is allied to *G. juncea* and is very similar to this species in general appearance, but differs in having pale mauve flowers, linear leaves with raised margins and midrib, more or less oblong in section and considerably larger flowers than are typically found in *G. juncea* which has terete leaves and white-, cream-, or yellow-colored flowers. *Geissorhiza purpurascens* is apparently a rare endemic of sandy soils between Stellenbosch and the coast at Mamre and Darling, where it has been collected at Bokbaai. It occasionally appears as an exhibit on the Darling Wild Flower Show, as it did in September 1981, when I obtained a live plant for description and illustration. Its habitat has not been recorded, but I was told that it grew in damp low lying places and on the edge of vleis. A search for the species which I made in 1981 proved futile. It must be considered endangered and further efforts should be made to discover and learn more about the species before it is lost.

A collection from the south slopes of the Piketberg, *Loubser 2177,* appears to belong here but it is unusual in having very broad leaves, to 5 mm wide, and flowers with a somewhat longer perianth tube than the populations to the south, which have leaves only 2–3 mm wide. The Piketberg population is reported to grow in stony well-drained soil.

Specimens examined. SOUTH AFRICA. CAPE: 3218 (Clanwilliam) Piketberg, along the road to Velddrif (DC), *Loubser 2177* (BOL).

3318 (Cape Town) Mamre hills (AD), *van Niekerk 258* (NBG); Mamre road (CB-DA), *Barker 808* (NBG); Bokbaai (CB), *Joubert 550* (PRE, STE); Burgers Pos farm near Pella, well-drained sand (DA), *Boucher & Shepherd 4815* (STE); Agter Paarl (DC), *Barker 402* (NBG); near Bottelary road, sandy soil (DC-DD), *Acocks 2163* (S).

WITHOUT PRECISE LOCALITY: Darling Flower Show, 1982, *Goldblatt s.n.* (MO).

27. **Geissorhiza humilis** (Thunb.) Ker, Ann. Bot. (König & Sims) 1: 242. 1804; Lewis, Fl. Cape Penins. 254. 1950. *Ixia humilis* Thunb., Diss. de *Ixia* no. 4: 141. 1783. TYPE: South Africa. Cape: hills around Cape Town, *Thunberg s.n.* "*I. humilis* α" [lectotype, Herb. Thunb. 959 UPS, designated by Brown (1928); isolectotype, Montin"] S "Herb. Casstrom, Herb. [*I. humilis* β, γ, and δ are different species (Goldblatt, 1982)]. FIGURE 40.

Geissorhiza humilis var. *humilis,* Baker, Fl. Cap. 6: 67. 1896, pro parte; Foster, Contr. Gray Herb. 135: 18. 1941.

Geissorhiza humilis var. *grandiflora* Baker, Handb. Irid. 153. 1892, Fl. Cap. 6: 67. 1896. TYPE: South Africa. Cape: fields near Claremont, *H. Bolus 4602* (lectotype, K, here designated; isolectotypes, BM, BOL, SAM); *Niven s.n.* (syntype, not seen); Cape flats *Pappe s.n.* (syntype, BM).

Plants short, 8–14 cm high. *Corm* asymmetric, ovoid, obliquely flattened below, projecting downward for a short distance, tunics light brown, concentric, fragmenting irregularly, drawn into bristles above. *Cataphyll* membranous, sometimes apparently lacking. *Leaves* 2–3, lowermost basal and longest, falcate, longer than the stem, the margins and midrib thickened and with 2 narrow grooves running the length of each surface, a second basal leaf often present and similar but smaller, the third leaf basal or more often cauline, sheathing below, ribbed, sometimes much reduced and becoming bract-like, all leaves (and bracts) sticky, and with sand adhering even when dry. *Stem* inclined, flexed above the base, rarely with a single branch. *Spike* 2–8-flowered, flexuose; *bracts* green, 8–12 mm long, lightly ribbed, margins hyaline, truncate, the inner as long, but smaller than the outer, sticky, and often covered with sand. *Flower* stellate, tepals spread horizontally when fully open, bright yellow; *perianth tube* 5–6 mm long, widening slightly at base, usually just exserted from bracts; *tepals* obovate,

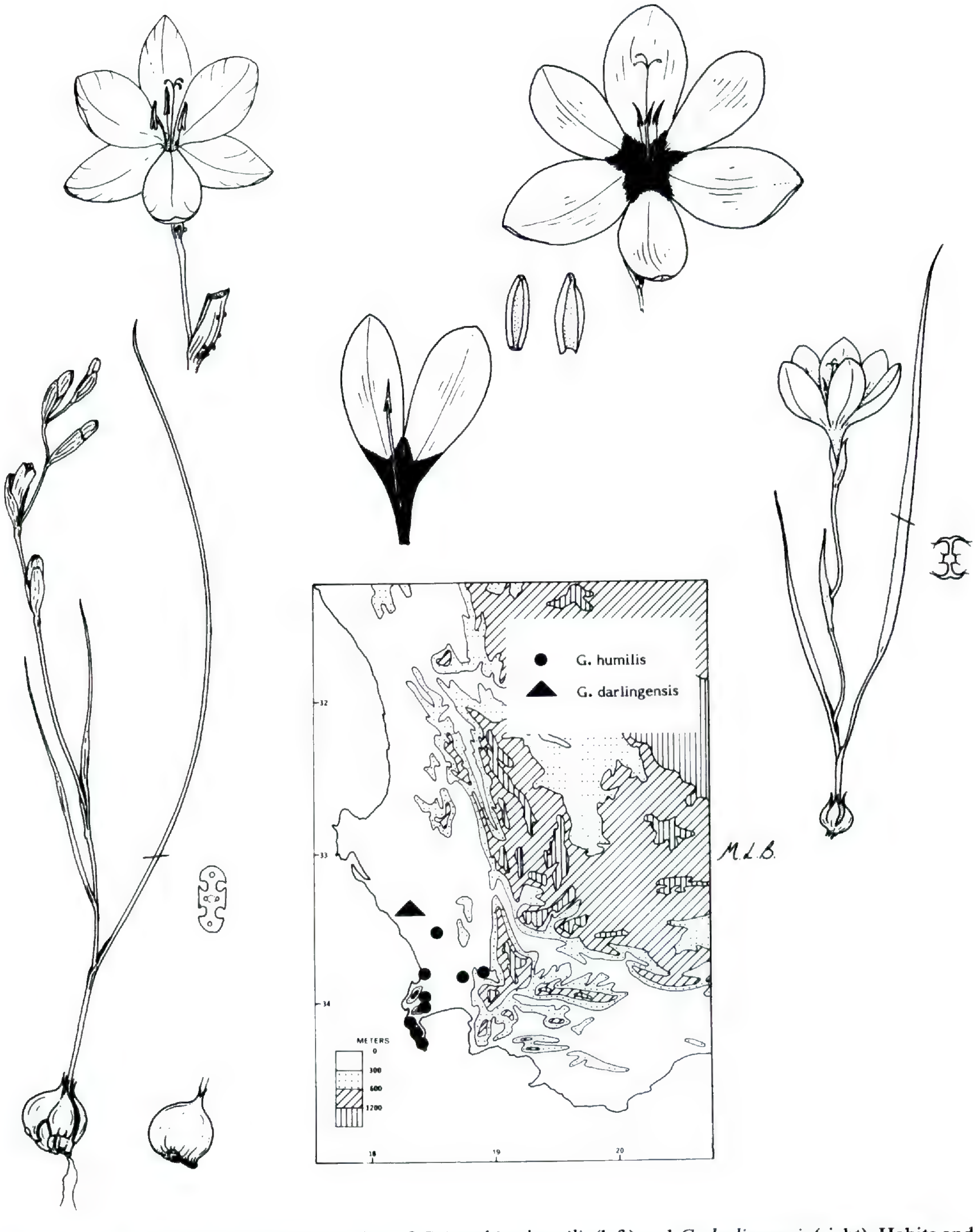


FIGURE 40. Morphology and distribution of *Geissorhiza humilis* (left) and *G. darlingensis* (right). Habits and corm ×0.5; flowers, separated bracts, and tepals life size; leaf sections much enlarged (*G. humilis*, flowering *Goldblatt 4125*, near Kommetje, fruiting *Goldblatt 5265*, foot of Klaasjagersberg; *G. darlingensis*, *Roux s.n.*, Versveld Reserve, Darling, ex hort.).

16–22 mm long, to 14 mm wide. *Filaments* ca. 5 mm long, erect; *anthers* ca. 5 mm long, yellow. *Ovary* 2–3 mm long; *style* dividing towards the apex of the anthers, branches 3–4 mm long, recurved. *Capsule* oblong-cylindric, (8–)10–12 mm long, shorter than or just exceeding the bracts, apparently dehiscent in the upper part only. *Chromosome number*, $2n = 26$ (*Goldblatt 5265*).

Flowering time. Late August to October.

Distribution. Sandy flats and mountain plateaus, Cape Peninsula and locally north across the Cape Flats. Figure 40.

Geissorhiza humilis is a rare species restricted to the Cape Peninsula and surrounding Cape Flats extending as far inland as Simondium, near Paarl. It grows on coarse sandy soil and flowers well only in the season following a veld fire when its golden yellow flowers make a conspicuous display. *Geissorhiza humilis* and the related smaller flowered *G. hispidula* grow together at several sites on the Cape Peninsula, and often flower at the same time. They are clearly quite different species when seen alive, although vegetative parts are difficult to distinguish, but the two have long been confused. *Geissorhiza hispidula* has until now been regarded either as a paler flowered form or as a distinct variety of *G. humilis*. Baker placed specimens regarded here as *G. humilis* in both *G. humilis* var. *humilis* and var. *grandiflora* while treating *G. hispidula* either as *G. humilis* var. *bicolor* or var. *humilis*. Foster, however, clearly distinguished the two and treated the smaller flowered and paler colored plants as var. *hispidula* or var. *bicolor*. Both varieties are here placed in *G. hispidula* (Foster) Goldbl.

Geissorhiza humilis has comparatively large golden yellow flowers with tepals to 22 mm long and a tube 5–6 mm long. The spikes may have as many as eight flowers, but more often plants are shorter and have fewer blooms. In contrast, *G. hispidula* has smaller cream-colored flowers, conspicuously marked red on the reverse of the outer tepals. The tepals are 10–15 mm long and the tube 3–4 mm long while the spikes usually have 2–5 flowers.

Geissorhiza darlingensis, a poorly known endemic of the Darling area to the north of the Cape Peninsula, is clearly closely allied to *G. humilis* and appears to be a local segregate of this species. *Geissorhiza darlingensis* has larger flowers that have tepals 23–26 mm long and a tube 9–11 mm long. The bright yellow flowers have a conspicuous dark center and this together with their large size makes the species easy to distinguish from *G. humilis*. A particularly robust form of *G. humilis* from Riverlands near Dassenberg, *Burgers 2595*, approaches *G. darlingensis* and appears to be intermediate between the two species. However, the flower does not have the dark center characteristic of the latter.

Specimens examined. SOUTH AFRICA. CAPE: 3318 (Cape Town) fields near Claremont, Cape Town (CD), *H. Bolus 4602* (BM, BOL, K, SAM); Claremont, *Dümmer 436* (E), *327* (E), *Salter 2772* (BM); Kenilworth Race Course, *Lewis 55* (SAM); flats near Blaauwberg, *Zeyher 428* (SAM); Wynberg, *Schlechter 1559* (B, G, M, W, Z); Riverlands near Dassenberg, sandy flats (DA), *Burgers 2595* (STE); Simondium (DD), *Stanford s.n.* (BOL 31903); Bottelary road, towards Railway, *Acocks 818* (S).

3319 (Simonstown), sandy slopes near Kommetje (AB), *Goldblatt 4125* (K, MO, PRE); Bergvliet farm, *Purcell s.n.* (SAM 93390); Klein Slangkop, *Wolley Dod 3033* (K, MO); Tokai, *Guthrie 1096* (BOL); S Peninsula, *Goldblatt 447* (BOL); Fish Hoek flats, *Levyns s.n.* (CT); Fish Hoek, *Wolley Dod 1616* (BOL, K); Bonteberg, Cape Peninsula, *Barker 816* (NBG); lower slopes of Klaasjagersberg, opposite Reserve, *Goldblatt 5265* (K, MO, NBG); Redhill, Simonstown, *Taylor 5247* (PRE); Simons Bay, *Wright 253* (GH, K); near Smitswinkel Bay (AD), *Hutchinson 670* (K); Smitswinkel Ridge, *Salter* 331/17 (BM); Olifantsbos, *Lewis 1075* (SAM); Cape Flats (BA), *Zeyher 3964* (K, SAM), *Pappe s.n.* (BM, K); Krom River, Cape Peninsula, *Barker 3880* (BOL, NBG); Kogelfontein, Cape Point Reserve, *Taylor 10025* (MO, STE).

WITHOUT PRECISE LOCALITY: Cape of Good Hope, *Bowie s.n.* (G); Hottentots Holland and Cape Flats, *Bowie s.n.* (BM), *Thunberg s.n.* "*Ixia setacea* β" (UPS), *Niven s.n.* (K).

28. Geissorhiza darlingensis Goldbl., sp. nov. TYPE: South Africa. Cape: Versveld Flower Reserve, Darling, cult. Nat. Bot. Gard., *Roux s.n.* (holotype, NBG; isotype, MO). FIGURE 40.

Planta 7–15 cm alta, tunicis cormi concentricis, foliis 3, duobus inferioribus basalibus, linearibus 4-sulcatisque, superiore infra caulem vaginante, spica 2–5 florum, floribus campanulatis, luteis centralibus atropurpureis, tubo 8–11 mm longo, tepalis 23–26 mm longis, antheris ca. 5 mm longis, stylo diviso prope apicem antherarum, ramis recurvatis.

Plants 7–15 cm high. *Corm* more or less symmetric, 5–8 mm diam., tunics pale brown, fragmenting irregularly, drawn into points above. *Cataphyll* membranous. *Leaves* 3, the lower two basal, linear, 2–3 mm wide, the margins and midrib much enlarged and minutely ciliate along the edges, with 2 wide grooves running the length of the leaf, slightly sticky and with some sand adhering, the lowermost longest, exceeding the spike, the uppermost leaf inserted on the stem above the ground, inflated and sheathing below, linear above. *Stem* erect below, flexed above the cauline leaf sheath and inclined, simple or with 1–2 branches. *Spike* 2–5-flowered, flexed at the base; *bracts* herbaceous, 10–15 mm or more,

truncate, the inner smaller. *Flower* somewhat cupped, pale yellow with a dark purple center; *perianth tube* nearly cylindric, 9–11 mm long, usually shortly exserted from the bracts; *tepals* 23–26 mm long, obovate, to 12 mm wide. *Filaments* 8–9 mm long; *anthers* 5 mm long, yellow. *Ovary* 2–3 mm long, *style* dividing near the apex of the anthers, branches 3 mm long, recurved. *Capsule* oblong, truncate, 10–12 mm long. *Chromosome number,* unknown.

Flowering time. Late September to mid-October.

Distribution. Damp sandy soil, known only from the Flora Reserve at Darling. Figure 40.

This striking species is apparently endemic to a small area near the town of Darling, north of Cape Town. It has been collected only rarely by both W. F. Barker and G. J. Lewis, on the same day in the Flora Reserve just outside Darling and years later by J. Roux. The very large pale yellow flower with a purple center is reminiscent of *Babiana pygmaea* (Iridaceae), a species also endemic to this area. This seems to be yet another example of floral mimicry which appears to be a common phenomenon in *Geissorhiza*. *Geissorhiza darlingensis* has a small corm with concentric tunics and clearly belongs in subgenus *Weihea*. It appears to be closely allied to *G. humilis,* a yellow-flowered species which occurs to the south on the Cape Peninsula and on the Cape Flats. *Geissorhiza humilis* has a smaller, self-colored flower, with a shorter perianth tube, and a similar four-grooved leaf which lacks entirely the leaf ciliation characteristic of *G. darlingensis*.

Specimens examined. SOUTH AFRICA. CAPE: 3319 (Cape Town) Versveld Flower Reserve, Darling (AD), *Barker 8656* (NBG), *Lewis 5086* (NBG), *Roux s.n.* (MO, NBG).

29. Geissorhiza hispidula (Foster) Goldbl., comb. et stat. nov. *Geissorhiza humilis* var. *hispidula* Foster, Contr. Gray Herb. 135: 19. 1941; Lewis, Fl. Cape Penins. 255. 1950. TYPE: South Africa. Cape: Cape Flats, *Zeyher 1599* (holotype, K; isotypes, B, G, K, SAM). FIGURE 41.

Geissorhiza setacea (Thunb.) Ker sensu Ker, Bot. Mag. 31: tab. 1255. 1810.

Geissorhiza humilis var. *bicolor* Baker, Handb. Irid. 153. 1892, Fl. Cap. 6: 67. 1896; Foster, Contr. Gray Herb. 135: 19. 1941; Lewis, Fl. Cape Penins. 255. 1950. TYPE: South Africa. Cape: Muizenberg, *MacOwan s.n. in Herb. Norm. Aust. Afr. 257* (lectotype, K; isolectotypes, B, BOL, G, SAM; syntypes, see Fl. Cap. 6: 67. 1896).

Geissorhiza plicata Pappe ms. (*Zeyher 1599*).

Geissorhiza brehmii Ecklon ms. [*Zeyher 1599* (78.9)].

Geissorhiza striata Ecklon ms. (*Ecklon & Zeyher Irid. 296*).

Plants small, 7–15(–25) cm high. *Corm* asymmetric, ovoid, 5–7 mm diam., base obliquely flattened on one side, sometimes extending downward shortly, tunics concentric, woody, brown. *Cataphyll* solitary, membranous. *Leaves* 3, rarely 2, the lower two longest, basal, erect to falcate, linear, 1–2 mm wide, slightly longer than the stem, margins and midrib much enlarged, with 2 narrow grooves running the length of each surface, edges of margin and midrib smooth or minutely ciliate, leaves and bracts often sticky, and with sand adhering even when dry, the lowermost longest, the uppermost cauline, usually short and sheathing below, sheathing part ribbed, and sometimes also ciliate along ridges. *Stem* more or less erect, rarely branched, bearing a single small, sometimes bract-like leaf. *Spike* 1–5-flowered, flexuose; *bracts* herbaceous with a hyaline or reddish margin, 7–9 mm long, sticky, the inner shorter than the outer. *Flower* stellate, white to cream, often with the reverse of outer tepals pink to red-flushed, tepals spreading when fully open; *perianth tube* 3–4 mm long, shorter than or just longer than the bracts; *tepals* 10–15 mm long, narrowly obovate, 5–8 mm wide. *Filaments* 3–4 mm long, erect; *anthers* yellow, ca. 3 mm long. *Ovary* 2–3 mm long, *style* dividing at the apex of the anthers, branches 2.5–3 mm long, recurved. *Capsule* obovoid to oblong, 5–8 mm long, exceeding the bracts, dehiscent at least to midline. *Chromosome number,* $2n = 26$ (*Goldblatt 5377*).

Flowering time. August to September.

Distribution. Cape Peninsula east to the Riversdale district, in sandy soil, usually on flats or mountain plateaus and flowering only in the season after a fire. Figure 41.

Geissorhiza hispidula has a relatively wide distribution extending from the Cape Peninsula east to the Riversdale district but it is common only in the west, where it is frequently found in sandy flat areas in the season following a veld fire. It has often been confused with the related *G. juncea* and *G. humilis* and both Baker (1892, 1896) and Foster (1941) included it as a variety of *G.*

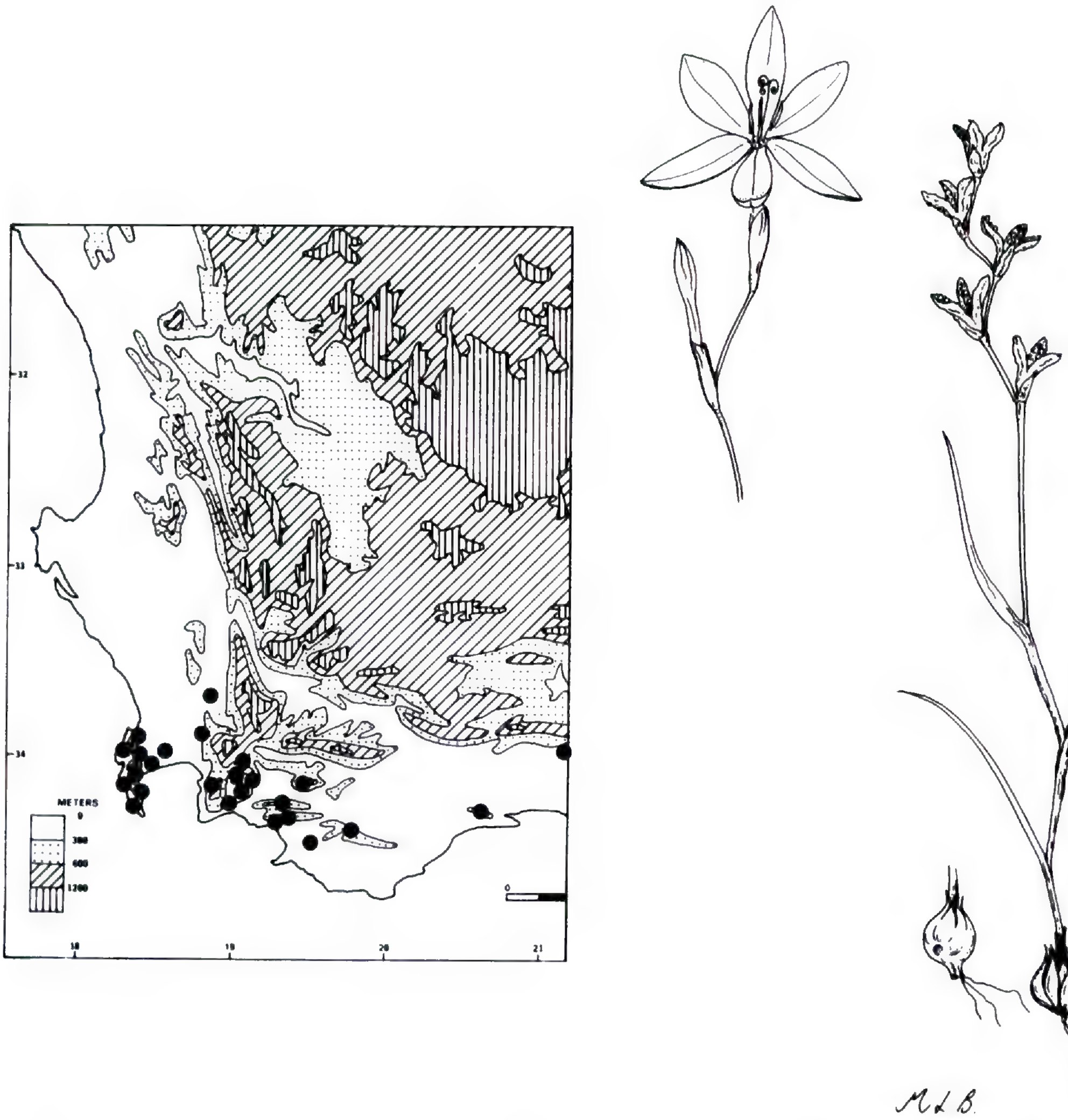


FIGURE 41. Morphology and distribution of *Geissorhiza hispidula*. Corm, fruiting, and flowering plants life size; leaf section much enlarged (fruiting *Goldblatt 5266*, foot of Klaasjagersberg, flowering *Goldblatt 4126*, near Kommetje).

humilis. Baker was particularly confused about the species and cited specimens of *G. hispidula* under *G. humilis* var. *humilis* and var. *grandiflora*, the latter corresponding exactly to the type of *G. humilis*. Foster clearly distinguished it from var. *humilis*, but assigned specimens here referred to *G. hispidula* to two nearly identical varieties, var. *hispidula* and var. *bicolor*, the latter differing only in having the leaf margins smooth rather than minutely ciliate-hispid. Careful examination of material Foster placed in var. *bicolor* has revealed that he failed to observe very inconspicuous cilia in some specimens. I prefer not to recognize the two varieties as the presence or absence of minute leaf ciliation seems a trivial distinction.

There seems little doubt that *Geissorhiza hispidula* is quite distinct from *G. humilis*. The latter has larger bright yellow flowers, is generally more robust and has broader leaves and it can readily be distinguished from *G. hispidula* on these characters (see discussion under *G. humilis*). Both species occur together at several places on the Cape Peninsula and although they flower simultaneously, they remain distinct from one another. When seen alive, it becomes clear that they are separate, although related species.

Specimens examined. SOUTH AFRICA. CAPE: 3318 (Cape Town) Table Mt., lower plateau (CD), *Wolley Dod 1774* (BOL), *Goldblatt 6725* (MO); Table Mt., Weather Station, *Werdermann & Oberdieck 17* (B, K, PRE); lower slopes above Camps Bay, *Lewis 1199*

(SAM); Raapenberg, Mowbray, *Guthrie 1095* (BOL); Claremont, *Schlechter 1568* (B, G, W, Z); E end of Table Mt. near Constantia, *Ecklon & Zeyher Irid. 296* (FI, MO); Wynberg flats, *Prior s.n.* (K); between Paarl and Pont (DB), *Drège 8475* (K); Stellenbosch flats (DD), *Garside 1066* (K).

3418 (Simonstown) Bergvliet (AB), *Purcell s.n.* (SAM 90342, 93391); lower slopes of Klaasjagersberg, opposite Cape Point Reserve, *Goldblatt 5266* (MO, PRE); sandy slopes near Kommetje, *Goldblatt 4126* (K, MO, PRE, US, WAG); near marsh at source of Slangkop River, *Wolley Dod 3190* (BM, BOL, K); Constantia corner, *Pillans 10776* (MO), *Salter 9483* (BM); Simonstown, *Zeyher 114* (BOL, SAM); top of Muizenberg Mt., *MacOwan s.n.* (or *2474*) *Herb. Norm. Aust. Afr. 257* (B, BM, BOL, G, GH, K, SAM), *MacOwan 2474* (S); Steenberg plateau, *Lewis 1198* [PRE (as SAM 57331), SAM], *Compton 13642* (NBG); Redhill, Simonstown, *Taylor 5246* (PRE), *Lewis s.n.* (PRE, SAM 61718, STE); near Cirkels Vlei, Cape Point Reserve (AD), *Lewis 1200* (SAM); Wynberg flats (BA), *Marloth 7162* (PRE), *Prior s.n.* (GH); Cape Flats, *Zeyher 1599* (B, BM, FI, G, K, P, S, SAM, W, Z); Kogelberg (BB), *Stokoe s.n.* (SAM 59846); Palmiet River mouth (BD), *Gillett 4236* (MO).

3419 (Caledon) foot of Houw Hoek Pass (AA), *Goldblatt 5639* (MO); foot of Viljoens Pass at Elgin, *Gillett 4459* (BOL); above Houw Hoek, *Gillett 4287* (BOL, K); Zwartberg, Caledon, 2,500 ft. (AB), *Galpin 4672* (PRE); Shaws Mt., *Barker 8* (BOL, K); Highlands Forest Reserve (AC), *Leighton 279* (BOL), *Compton 13481* (NBG), *Goldblatt 4783* (MO); Lebanon Forest Reserve, catchment IId, *Kruger 487* (STE, PRE); Fernkloof Nature Reserve, Hermanus (AD), *Orchard 280* (BR, K, S, STE), *483* (MO); Hermanus, E side of the Vogelgat River, *S. Williams 840* (MO), *Goldblatt 7034* (MO); Sandys Glen, burned area (BD), *Goldblatt 4849A* (MO, WAG); Papiesvlei fynbos, *Acocks 22791* (PRE); farm Paardeberg, Papiesvlei, *Taylor 4055* (PRE); Strandkoof (CB), *Compton 21971* (NBG).

3420 (Bredasdorp) Potberg Mt., upper slopes in black sand (BC), *Burgers 2446* (STE).

3421 (Riversdale) summit of hills behind Albertinia (BA), *Muir 1835* (BOL).

WITHOUT PRECISE LOCALITY: South Africa, *Sieber 395* (MO); Capstadt, *Spielhaus 1877* (B); Cap. Bonae Spei, *Lalande s.n.* (B).

30. Geissorhiza pappei Baker, Handb. Irid. 154. 1892, Fl. Cap. 6: 68–69. 1896; Foster, Contr. Gray Herb. 135: 20–21. 1941. TYPE: South Africa. Cape: Zonder Einde Mts., *Zeyher 3965* [lectotype, K; designated by Foster (1941); isolectotypes, B, SAM]; *Pappe s.n.*, *Zeyher 3967* (syntypes, not seen).

Plants small, 5–10 cm high. *Corm* asymmetric, ovoid, 5–7 mm diam., the base obliquely flattened on one side, tunics concentric, soft and papery, light brown. *Cataphyll* solitary, membranous, sticky and usually covered with sand. *Leaves* 3, rarely 2, the lower two basal, erect to falcate, linear, 0.5–1.3 mm wide, the margins and midrib somewhat to much enlarged and then with 2 narrow grooves running the length of each surface, the edges of margin and midrib evidently smooth, leaves (and bracts) often sticky and with sand adhering even when dry, the lowermost leaf longest and somewhat longer than the stem, the second shorter, the uppermost cauline, usually short and sheathing below, occasionally reduced and bract-like, the sheathing part ribbed. *Stem* more or less erect, rarely branched, bearing a single small, sometimes bract-like, leaf. *Spike* 1–4-flowered, flexuose; *bracts* herbaceous, hyaline above, 3–6 mm long, the inner shorter than the outer. *Flower* stellate, white to cream, tepals spreading when fully open; *perianth tube* 2.5–3.5 mm long, shorter than or just longer than the bracts; *tepals* 6–9 mm long, narrowly obovate, 2.5–4 mm wide. *Filaments* ca. 2 mm long, erect; *anthers* yellow, ca. 2 mm long. *Ovary* 1.5–2 mm long, *style* dividing at the apex of the anthers, branches to 0.7 mm long, recurved. *Capsule* unknown. *Chromosome number,* unknown.

Flowering time. September to early October.

Distribution. Apparently rare and local in the southwestern Cape, from Riviersonderend in the east to Ceres in the north, in sandy soil. Figure 42.

There is some doubt whether *Geissorhiza pappei* is distinct from the more widespread and common *G. hispidula.* This species has larger, cream to yellow flowers, usually marked red on the reverse of the outer tepals, is generally more robust and has broader leaves and larger corms with brittle woody tunics. While *G. pappei* can readily be distinguished from *G. hispidula* by comparing these characters, there is a possibility that *G. pappei* may be simply a depauperate form of the more robust *G. hispidula.* Baker (1892), who described the species in his "Handbook of the Irideae," continued to recognize it in "Flora Capensis" (1896) and Foster (1941) also included it in his monograph of the genus. While I have doubts about its status, I prefer not to alter the current treatment until more evidence becomes available.

Geissorhiza pappei has a limited distribution in the southwestern Cape. It has been collected near Riviersonderend, at Highlands in the Caledon district and at Ceres. It is probably more common than the record indicates but it is very inconspicuous and it may often have been overlooked.

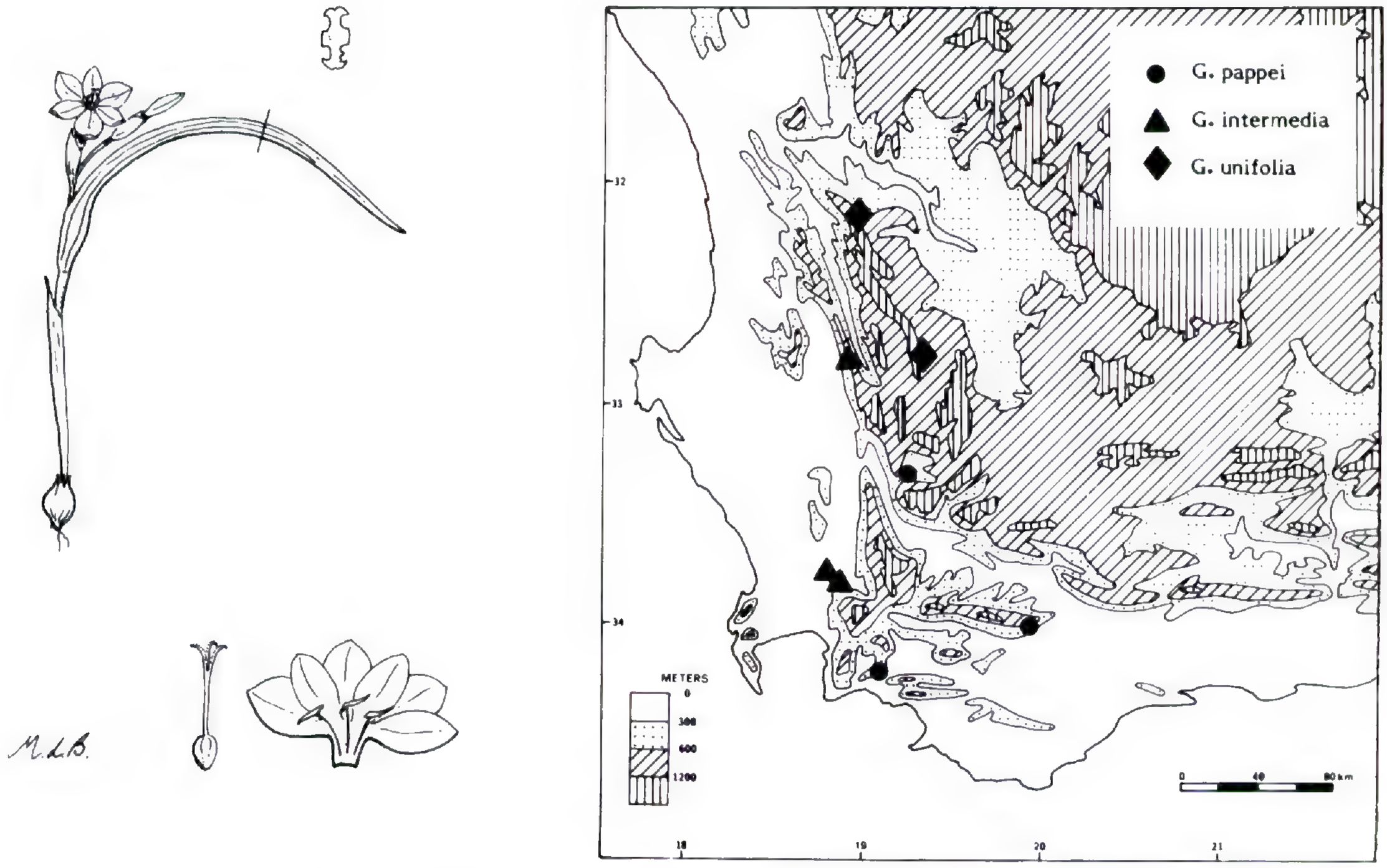


FIGURE 42. Morphology of *Geissorhiza unifolia* and distribution of *G. pappei, G. intermedia,* and *G. unifolia.* Habit life size; flower and gynoecium ×2; leaf section much enlarged (*Esterhuysen 36128,* Bokkeveld Sneeuberg).

Specimens examined. SOUTH AFRICA. CAPE: 3319 (Worcester) Ceres, foot of mt. near village (AD), *Marloth 12996* (PRE).

3419 (Caledon) Highlands (AC), *Compton 13480* (NBG); Zonder Einde Mts. (BB), *Zeyher 3965* (B, K, SAM).

31. Geissorhiza intermedia Goldbl., sp. nov. TYPE: South Africa. Cape: Banhoek, Spitzkop, 4,000 ft., *Esterhuysen 11887* (holotype, BOL).

Planta 5–12 cm alta, foliis 3, inferiore longissimo, basali, 1.5–3.5 mm lato, marginibus et costis incrassatis quadrisulcatisque, superiore infra caulem vaginante, caule erecto ciliato raro ramoso, spica 1–3 florum, floribus stellatis albis, tubo ca. 3 mm longo, tepalis 8–10 mm longis, antheris 2–3 mm longis, stylo diviso prope apicem antherarum, ramis recurvatis.

Plants small, 5–12 cm high. *Corm* ovoid, 5–7 mm diam., tunics concentric, firm textured, light brown. *Cataphyll* solitary, membranous. *Leaves* 3, erect and ensiform or falcate, 1.5–3.5 mm wide, about as long as the stem, the margins and midrib enlarged and with 2 broad grooves running the length of each surface, the margin and midrib edges evidently smooth (but sometimes sparsely and minutely ciliate), the lower two leaves basal, the lowermost longest and often slightly sticky below and on the sheath, and with sand adhering even when dry, the second much shorter, the uppermost leaf smallest, cauline, sheathing below. *Stem* minutely and densely ciliate above the uppermost leaf, more or less erect, rarely branched. *Spike* 1–3-flowered, flexuose; *bracts* herbaceous, hyaline above, 6–9 mm long, the inner 1–2 mm shorter than the outer. *Flower* stellate, white, tepals spreading when fully open; *perianth tube* 2–3 mm long, not reaching the apex of the bracts; *tepals* 8–10 mm long, narrowly obovate, ca. 4 mm wide. *Filaments* ca. 4 mm long, erect; *anthers* yellow, 2–3 mm long. *Ovary* ca. 2 mm long, *style* dividing at the apex of the anthers, branches to 2 mm long, recurved. *Capsule* unknown. *Chromosome number,* unknown.

Flowering time. September to October.

Distribution. Apparently rare and local in the southwestern Cape, recorded only from Banhoek and Simonsberg in the south and on the Twenty Four Rivers Mountains in the north, in sandy soil. Figure 42.

Geissorhiza intermedia is apparently a rare montane species of the southwestern Cape mountains and it is known from only three collections. It stands out in subgenus *Weihea* in its densely ciliate stem, an unusual character in this subgenus. *Geissorhiza intermedia* is otherwise

undistinguished and its white flower with a well-developed perianth tube and narrow leaf with strongly raised margins and midrib are typical of section *Angustifolia,* to which it has been assigned. It can easily be mistaken for the similar and probably closely related *G. hispidula* which has a lowland distribution, and can be distinguished by its narrower, sticky leaf, sticky bracts, and invariably smooth stem. *Geissorhiza intermedia* may also be confused with *G. similis,* which is similar in its leaf and general appearance but has imbricate corm tunics, a longer perianth tube, and also has smooth stems. There is also a strong resemblance between *G. intermedia* and the Cedarberg endemic, *G. ciliatula,* but this species has smaller flowers that turn blue on fading, narrow leaves, the second of which sheaths the stem in its lower half, and is altogether a much more slender plant.

Specimens examined. SOUTH AFRICA. CAPE: 3318 (Cape Town) Simonsberg (DD), *Rehm s.n.* (M); Banhoek, Spitzkop, crevices and foot of cliffs, 4,000 ft., *Esterhuysen 11887* (BOL).

3319 (Worcester) Twenty Four Rivers Mts., rocky koppie on plateau (AA), *Esterhuysen 23769* (BOL).

32. Geissorhiza unifolia Goldbl., sp. nov. TYPE: South Africa. Cape: N Cedarberg, Peak at Koupoort, *Esterhuysen 12159* (holotype, BOL; isotype, MO). FIGURE 42.

Planta parva 5–10 cm alta, cormis ca. 5 mm diam., tunicis fragilis papyraceis manifeste concentricis, folio uno basali, marginibus costisque incrassatis, caule erecto papilloso-ciliato, bracteam supra ferenti, spica 1–5 florum, floribus stellatis albis, tubo ca. 2 mm longo, tepalis ca. 5 mm longis, antheris ca. 1.8 mm longis, capsula globosa ad 4 mm longa.

Plants small, 5–10 cm high. *Corm* globose, ca. 5 mm diam., tunics pale brown, brittle papery, apparently concentric, notched below and drawn into bristles above. *Cataphyll* membranous, sticky, and with soil adhering. *Leaf* solitary (occasionally 2), basal, sheathing the stem below, linear to falcate, 0.5–1.3 mm wide, the margins and midrib thickened. *Stem* erect, flexed above the leaf sheath, minutely papillate-ciliate especially below, simple, bearing a short, submembranous sheathing bract in the upper third. *Spike* 1–5-flowered, flexuose; *bracts* 3.5–5 mm long, herbaceous below, dry and transparent to light brown above. *Flower* stellate, tiny, white, the outer tepals pink-purple on the reverse; *perianth tube* 1.5–2 mm long, cylindric; *tepals* 3.5–5 mm long, and to 2 mm wide. *Filaments* ca. 2 mm long; *anthers* 1–1.8 mm long. *Ovary* 1.3–2 mm long, *style* dividing at the midline of the anthers, branches ca. 1 mm long, recurved. *Capsule* globose, to 4 mm long, shorter than bracts. *Chromosome number,* unknown.

Flowering time. October.

Distribution. Local in the Cedarberg and Cold Bokkeveld Mountains, at high elevations on thin soils. Figure 42.

Geissorhiza unifolia is an unusual, dwarf species of the Cedarberg and Cold Bokkeveld Mountains. It is known only from two collections, both made by Elsie Esterhuysen, one in 1945 and the other in 1983. The species is apparently rare and restricted to high altitudes and grows on flat rocky pavement in thin soil and on south-facing slopes on damp ledges and rock cracks. It is easily recognized by its tiny flowers with tepals 5 mm long and single produced leaf. The minutely ciliate stem which bears a short membranous and entirely sheathing bract in the upper third and the sticky cataphyll to which soil adheres even when dry are also unusual features that distinguish the species.

It apparently belongs to subgenus *Weihea,* having concentric corm tunics very like those of *Geissorhiza pappei* in their brittle papery texture. *Geissorhiza unifolia* bears a superficial resemblance to depauperate specimens of *G. scillaris* (subgenus *Geissorhiza*) (e.g., *Stokoe s.n.,* Heuning Vlei) but even such dwarfed individuals of *G. scillaris* consistently have two produced leaves in addition to the characteristic membranous stem bract of this species. The affinities of *G. unifolia* may have to be reassessed when more material becomes available, but for the present it is assigned to section *Angustifolia* close to *G. pappei.*

Specimens examined. SOUTH AFRICA. CAPE: 3219 (Wuppertal) N Cedarberg, Peak at Koupoort, damp ledges and crevices on S side (AA), *Esterhuysen 12159* (BOL, K); Bokkeveld Sneeuberg, 6,600 ft., thin sand on rock pavement (CD), *Esterhuysen 36128* (MO, NBG, PRE).

33. Geissorhiza juncea (Link) A. Dietr., Sp. Pl. 6th edition, 2: 587. 1833; Foster, Contr. Gray Herb. 135: 21. 1941. *Ixia juncea* Link, Enum. Hort. Berol. Alt. 1: 50. 1821; Baker, J. Linn. Soc., Bot. 16: 93. 1878. *Geissorhiza humilis* var. d. *juncea* (Link) Baker, Handb. Irid. 153. 1892, Fl. Cap. 6: 67. 1896. TYPE: South Africa. locality unknown: cultivated in Berlin by Link, from material sent to him by Bergius in Stockholm (*Bergius s.n. Ixia*

setacea), *Link 1205* "*Ixia juncea* m" [lectotype, B, effectively designated by Foster (1941)]. FIGURE 43.

Geissorhiza filifolia Baker, J. Bot. n.s. 5: 238. 1876, Fl. Cap. 6: 68. 1896. TYPE: South Africa. Cape: precise locality unknown, *Prior s.n.* (or *Alexander s.n.*) (holotype, ? BM, not seen; GH, photo).

Geissorhiza secunda var. *setifolia* Ecklon ex Baker, Handb. Irid. 155. 1892, Fl. Cap. 6: 69. 1896. TYPE: South Africa. Cape: between Paarl and Pont, *Drège 8460* (lectotype, K, here designated; syntypes, several cited in Fl. Cap. 6: 69. 1896).

Geissorhiza setifolia Ecklon, Topogr. Verz. Pflanzensamml. Ecklon 22. 1827, nom nud.

Geissorhiza pallidiflora Schltr., Bot. Jahrb. Syst. 27: 97. 1899. TYPE: South Africa. Cape: damp sandy flats between Bains Kloof and Wolseley (Ceres Road), *Schlechter 9088* (lectotype, B, here designated; isolectotypes, B, BM, BOL).

Geissorhiza juncea var. *pallidiflora* (Schltr.) Foster non sensu Foster, Contr. Gray Herb. 135: 23. 1941, excl. specimens cited (intended for *G. scillaris* A. Dietr.).

Hesperantha subulata Baker, Bull. Herb. Boissier, Ser. 2, 1: 864. 1901. TYPE: South Africa. Cape: Cape Flats, *Rehmann 1850* (lectotype, Z, here designated; isolectotypes, BM, BR).

Ixia flexuosa L. sensu Thunb. pro parte, *Thunberg s.n.* (S).

Geissorhiza setacea (Thunb.) Ker sensu Klatt, Linnaea 34: 656. 1866, pro parte.

Plants slender, (7–)20–35(–45) cm high. *Corm* globose, 5–9 mm diam., tunics light brown, concentric, usually woody, the outer layers fractured irregularly, drawn into bristles above. *Cataphyll* dry, single, reaching the above ground, sticky and often covered with sand. *Leaves* usually 3, the lower two basal, terete, erect, reaching to about the middle of the spike, with 4 narrow longitudinal grooves, the third inserted above the ground and sheathing the stem for about half its length, the free upper part 2–4 cm long, also terete. *Stem* erect, flexed at base of spike, and sometimes also above sheath of cauline leaf, usually simple, rarely with 1 branch and rarely with a membranous stem bract. *Spike* (1–)3–8(–13)-flowered; *bracts* 5–8 mm long, pale green to brown below, white and membranous above, curving outwards in the upper half, the inner 4–6 mm long, shorter than the outer. *Flowers* stellate, white or cream to pale yellow, outer tepals often reddish or brown on the reverse; *perianth tube* 2–3 mm long, infundibuliform; *tepals* (6–)8–12(–14) mm long, ovate, 3–5.5 mm wide. *Filaments* 2–3(–5) mm long; *anthers* 2–3(–4) mm long. Ovary ca. 2 mm long, *style* 6–12 mm long, dividing above the apex of the anthers, branches 1–2.5 mm long. *Capsule* globose, 3–4.5 mm long. *Chromosome number*, $2n = 26$ (*Goldblatt 4700*).

Flowering time. August to October (to November at high altitudes).

Distribution. Mountains and wet sandy flats from the Caledon district and Cape Peninsula north to Piketberg and the Cedarberg at Pakhuis Pass. Figure 43.

Geissorhiza juncea is a fairly common southwestern Cape species, most often encountered on sandy flats or slopes and occasionally also on damper clay or granite soil. It often grows in semi-marshy situations, or places extremely wet during the rainy winter and spring. The flowers are usually cream-colored with a red flush on the reverse of the outer tepals, but flowers may be nearly white, or yellowish and with or without a reddish flush on the reverse. The small flowers are in no way distinctive, and *G. juncea* is most readily recognized by its tall, slender habit with two, terete, basal, narrowly four-grooved leaves and third shorter, partly sheathing leaf inserted high up on the stem.

It has been confused at times with the unrelated, but superficially similar *Geissorhiza scillaris*, especially by Foster (1941), and specimens he cites as *G. juncea* var. *pallidiflora*, but not the type, are mainly referable to this species. *Geissorhiza scillaris* has nearly identical small, short-tubed, white or sometimes blue flowers but a single basal, subterete leaf; a second, almost entirely sheathing, either basal or cauline leaf; and a characteristic small, sheathing membranous stem bract below the spike. It can be distinguished on all of these characters from *G. juncea*. These two species are actually only distantly related, *G. juncea* having concentric and *G. scillaris* imbricate corm tunics (Goldblatt, 1983). *Geissorhiza juncea* is allied to a group of species including *G. humilis* and *G. hispidula* (section *Angustifolia*) which have small corms with hard concentric tunics and narrow leaves with raised and thickened margins and midribs and it can be readily distinguished from these species by its terete leaves. It is closely allied to *G. furva* a low growing species with moderate to large deep yellow flowers and similar narrow, terete leaves.

While *Geissorhiza juncea* typically has small, white- to pale yellow-colored flowers on slender spikes of six to ten blooms over most of its range, several collections comprise somewhat shorter plants with fewer and larger yellow flowers with

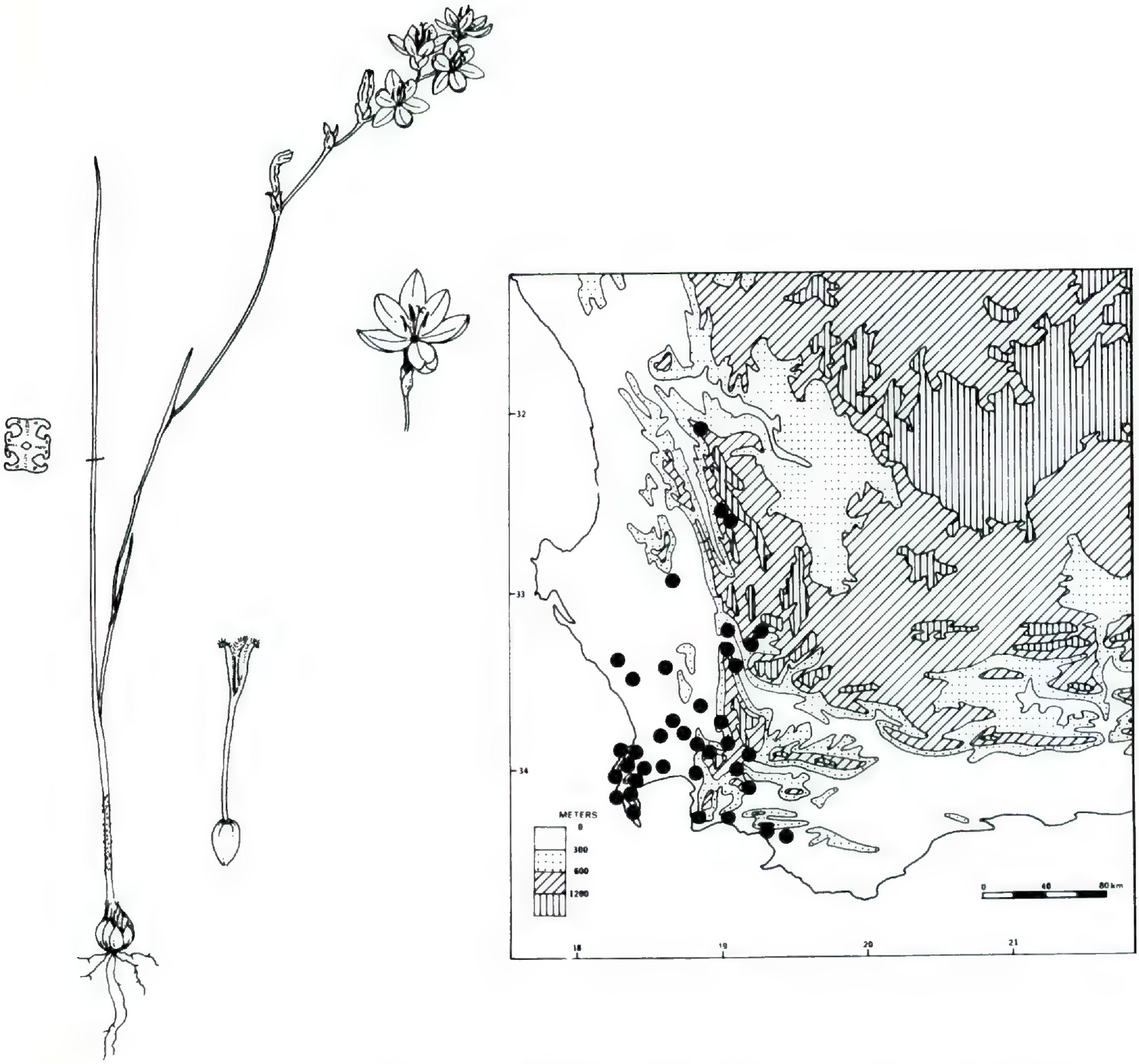


FIGURE 43. Morphology and distribution of *Geissorhiza juncea*. Habit ×0.5; flower life size; leaf section much enlarged (*Goldblatt 6283A*, Malmesbury Commonage).

tepals in the 12–14 mm range (*Walgate 381, Acocks 24412, Lewis & Davis 2231, Goldblatt 6283A*). These collections seem mainly to have come from areas of clay soils and they may be an ecotype adapted to this substrate. They intergrade with typical *G. juncea* and are not sufficiently distinct to merit taxonomic recognition. However, this larger flowered form approaches the related *G. furva* in many ways. *Geissorhiza furva* has deep yellow flowers with tepals 15–22 (–28) mm long on spikes of one to three blooms, and the plants are typically shorter than *G. juncea* being only 5–12(–18) cm high. The flowers of *G. furva* are distinctive when dry as they turn an unusual blackish color with age.

The taxonomy and nomenclature of *Geissorhiza juncea* have been much confused at times. The species was not distinguished from the superficially similar *G. scillaris* (the type sheet of which includes specimens of both species) by Thunberg and several subsequent authors (Goldblatt, 1983). Only in 1821 was this common Cape plant described and recognized as a distinct species. Ecklon (1827) clearly regarded the species as distinct but applied to it the name *G. setifolia*, a nomen nudum, nevertheless taken up by several authorities. Baker (1878) initially regarded *G. juncea* as a separate species but he also recognized as a new species, *G. filifolia* (of which I have only seen a photograph purporting to be the type) as well as *G. secunda* var. *setifolia*, both of which seem to differ in no significant way from

typical *G. juncea*. Later, Baker (1892, 1896) treated *G. juncea* as a variety of *G. humilis* while continuing to recognize both *G. filifolia* and *G. secunda* var. *setifolia*. Foster clarified the situation considerably, but he also failed to realize that *G. juncea* and *G. scillaris* were separate species, although he attempted to distinguish them at the varietal level.

Specimens examined. SOUTH AFRICA. CAPE: 3218 (Clanwilliam) hills near Berg River, Piketberg (DC), *Schlechter 5273* (B, BM, BOL, E, PRE, S, Z).

3319 (Wuppertal) Pakhuis Pass (AA), *Leipoldt s.n.* (STE); upper S-facing slopes of Pakhuis Pass, *Goldblatt 6398* (MO, NBG, S); Elands Kloof (CA), *Lewis s.n.* (BOL 31885), *Barker 3117* (NBG); Elands Kloof, marshy area, *Thompson 1542* (MO, PRE, STE); flats near entrance to Elands Kloof, *Esterhuysen 13013* (BOL).

3318 (Cape Town) Kapok Berg, Darling (AC), *H. Bolus 12841* (BOL); summit of Contreberg, *Pillans 6906* (BOL); Mamre hills, *Barker 1765* (NBG); stony outcrops near Darling, *Lewis 891* (SAM), Groene Kloof, *Zehyer 294* (SAM); Malmesbury commonage (BC), *Lewis 3630* (SAM), *Goldblatt 6283A* (MO, PRE); between Malmesbury and Mooreesburg, *L. Bolus s.n.* (BOL 20647, K); Devils Peak (CD), *Wolley Dod 3011* (BOL), *520* (BM, K); Table Mt., Disa Gorge, *Esterhuysen 17574* (BOL); Table Mt., *Ecklon 316* (MO, PRE, S), *H. Bolus 4615* (BOL, BR, GH, Z); W slopes of Lions Head, *Wolley Dod 2838* (BOL, K); slopes of Lions Head, above Round House, *Goldblatt 4700* (MO); Lions Head, *Wilms 3702* (B, L, PH); Platteklip Gorge, Table Mt., *Galpin 4689* (K, PRE); Table Mt., plateau, *Werdermann & Oberdieck 763* (B), *Goldblatt 5309* (MO), *5310* (MO); Table Mt., Llandudno Ravine, *Esterhuysen 35678* (C, E, M, MO, NU, PRE, WAG, US); Kenilworth Race Course, *Lewis 627* (SAM); 6.4 km WNW of Windmill (DB), *Acocks 24412* (MO, PRE); between Paarl and Pont, *Drège 8460* (K); Durbanville (DC), *Compton 16017* (NBG); Hercules Pillar (DD), *Barker 1768* (NBG); Bottelary road near Stellenbosch, *Lewis & Davis 2231* (SAM); Stellenbosch, *Duthie 586* (BOL); Jonkershoek, upper slopes of Ridge Peak, *Esterhuysen 32744A* (BOL); Jonkershoek, valley below The Twins, *Esterhuysen 34387* (BOL); Jonkershoek, *Taylor 5975* (STE), *5198* (PRE, STE).

3319 (Worcester) Mts. near Tulbagh Falls (AC), *H. Bolus 5388* (BOL, K); Tulbagh, *Pappe s.n.* (SAM 48576); valley above Tulbagh falls, *Esterhuysen 35064* (MO, PRE, US); sandy flats between Ceres Road (Wolseley) and Bains Kloof, *Schlechter 9088* (B, BM, BOL); Mts. above Ceres (AD), *Bayliss 6162* (MO); Prince Alfreds Hamlet, *Walgate 381* (NBG, SAM); Darling Bridge, *Lewis 4791* (PRE, SAM); between Worcester and Villiersdorp (CB-CC), *Barker 7538* (BOL, NBG, W); French Hoek (CC), *Phillips 1310* (SAM), *Barker 4176* (NBG); between French Hoek and Villiersdorp, *Lewis 2897* (SAM); Olifants Berg, *Gillett 1858* (BOL, STE); Drakenstein Mts., 2,000–3,000 ft., *Drège s.n.* (B, G, S).

3418 (Simonstown) Steenberg Plateau, *Lewis s.n.* (SAM 56866); Muizenberg, *Prior s.n.* (PRE); Orange Kloof, *L. Bolus s.n.* (BOL); Karbonkelberg, Hout Bay, *Stokoe s.n.* (SAM 60196); Kalk Bay Mt., *Barker 4223* (NBG); Noordhoek Mt., beside stream, *Barker 2353* (NBG); Skoorsteen Kop, Hout Bay, *Acocks 683* (PRE); Smiths Farm (AC), *Lewis 669* (SAM); Cirkels Vlei, Cape Point Reserve, *Compton 16333* (NBG); between Klaasjagers and Smitswinkel, *Wolley Dod 1508* (BM); Cape Point Reserve, veld near W Coast, *Goldblatt 422* (BOL); Cape Flats (BA), *Pappe s.n.* (SAM 48575), *Zeyher 3963* (B, SAM), *Rehmann 1850* (BM, Z); Somerset West (BB), *Zeyher s.n.* (SAM); rocky S slopes of Helderberg, *Esterhuysen 14661* (BOL, PRE); Sir Lowrys Pass Station, *Guthrie 2532* (NBG); between Rooi Els and Manganese mine (BD), *Boucher 1659* (STE); Palmietrivier, *Penther 605* (Z).

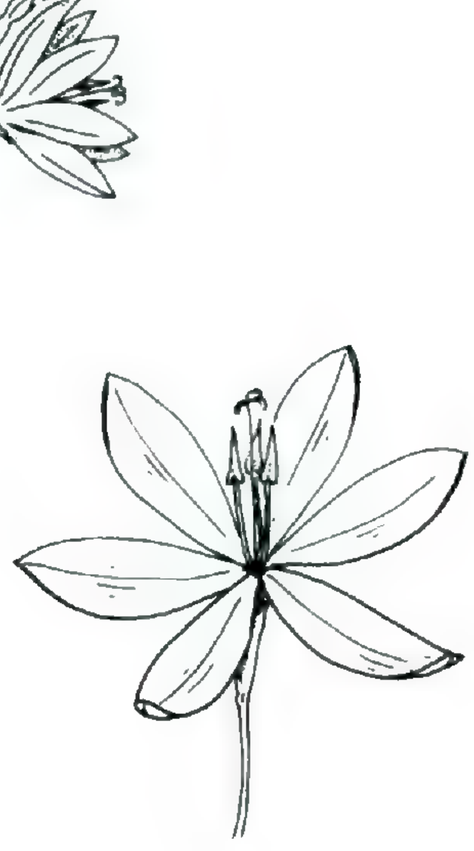
3419 (Caledon) 4 mi. N of Bot Rivier (AA), *Goldblatt 294* (BOL); flats E of Viljoens Pass, *Davis s.n.* (SAM 61721); Vogelklip, Hermanus (AD), *Barker 1790* (NBG); mt. slopes behind Voelklip, Hermanus, *Goldblatt 7040A* (MO); 2 mi. from Stanford near head of vlei, *Gillett 4450* (BOL, MO); Riviersonderend Mts. (B), *Stokoe s.n.* (SAM 63479).

WITHOUT PRECISE LOCALITY: between Malmesbury and Hopefield, *Salter s.n.* (BOL); Zwartland, *Bachmann 1090* (B); Cape of Good Hope (CBS), *Mund & Maire 506*, (B), *508* (B), *Niven s.n.* (BR), *Berguis s.n.* (B), *Link 1205* (B), *Lichtenstein 508* (B), *Siebold 573* (B), *Thunberg s.n.* (*Ixia flexuosa*) (S); Worcester, Tulbaghskloof, Tulbaghsthal, Witsenberg, und bei Vogelvalei, *Ecklon & Zeyher Irid. 217* (77) (B, BM "Tulbagh").

34. Geissorhiza furva Ker ex Baker, Handb. Irid. 155. 1892, Fl. Cap. 6: 70. 1896; Foster, Contr. Gray Herb. 135: 26–27. 1941. TYPE: South Africa. Cape: between Paarl and Pont, *Drège 8478* (lectotype, K, here designated; isolectotypes, G, L); *Masson s.n.* (syntypes, BM, K); *H. Bolus 4341* (syntype, not seen, location uncertain). FIGURE 44.

Geissorhiza furva Banks ex Ker, Ann. Bot. (König & Sims) 1: 224. 1804, nom. nud. (the Banks specimen annotated "*Ixia furva*" on which this name is based is at BM, was collected by Masson, and probably represents authentic material).

Plants small to medium, 7–18 cm high. *Corm* globose, more or less symmetric, but obliquely flattened below, 7–9 mm diam., tunics light brown, concentric, the layers fragmenting irregularly, drawn into bristles above. *Cataphyll* membranous, sticky and with sand adhering. *Leaves* 3 (rarely 2), evidently terete, narrowly 4-grooved, the lower two basal, the lowermost longest, usually slightly exceeding the stem, the second sheathing below, the uppermost cauline, sheathing the stem below, terete above, sometimes becoming short and bract-like. *Stem* erect, flexed above the leaf sheaths, and below the first flower. *Spike* 1–3-flowered, flexuose; *bracts* 6–12 mm long, herbaceous below, dry and papery above, the inner usually slightly smaller than the



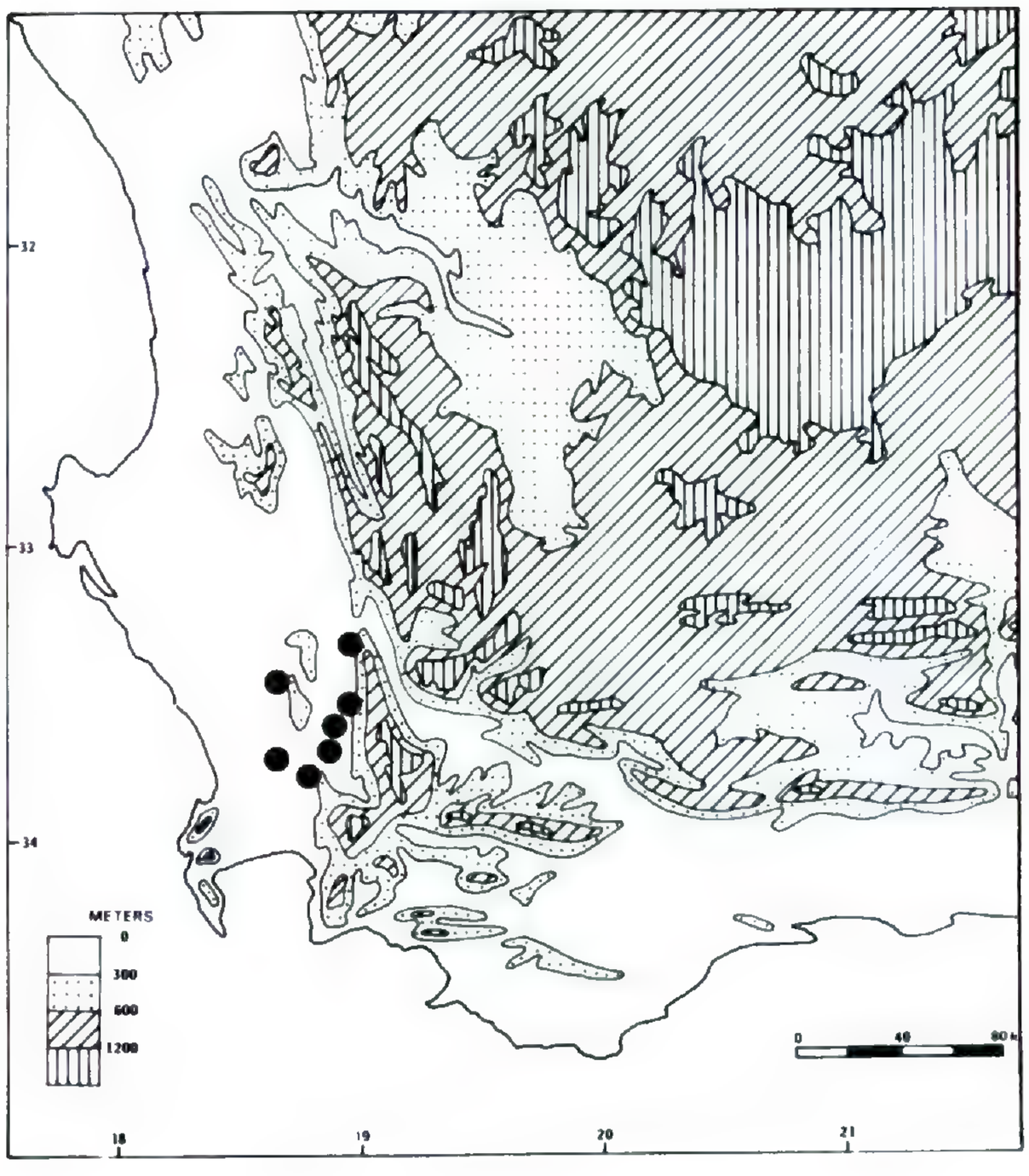


FIGURE 44. Morphology and distribution of *Geissorhiza furva*. Habit ×0.5; flower life size; leaf section much enlarged (*Goldblatt 6212*, foot of the Elandskloof Mts.).

outer, sometimes longer. *Flower* stellate, tepals spreading, deep golden yellow, becoming blackish when dry; *perianth tube* infundibuliform, (3–)4–5 mm long; *tepals* 15–22(–28) cm long, obovate, to 12 mm wide. *Filaments* 7–13 mm long, erect; *anthers* to 6 mm long, yellow. *Ovary* 2–4 mm long, *style* dividing near the apex of the anthers, branches to 5 mm long, recurved. *Capsule* unknown. *Chromosome number*, unknown.

Flowering time. September to mid-October.

Distribution. Southwestern Cape, stony or sandy situations along the foot of the mountains between Stellenbosch and Gouda. Figure 44.

Geissorhiza furva is closely related to the widespread, small-flowered *G. juncea*, with which it is almost identical in vegetative morphology. It has three terete leaves, the lower two more or less basal and the upper cauline and partly sheathing; an unbranched stem; and small corms with hard, concentric tunics. It is however distinctive in having a 1–3-flowered spike and large, deep yellow flowers, which when dry turn a very characteristic blackish color. *Geissorhiza furva* is apparently restricted to the Paarl and Wellington districts of the southwestern Cape, where it occurs on stony or sandy sites at the foot of the mountains that run north–south, parallel to the west coast. It is known from only a few sites and is now seriously endangered by agricultural expansion in the area where it occurs.

It varies considerably in height and flower size. Specimens collected by Compton (*11732*) and Leighton (*2002*) are 6–9 cm high with flowers having tepals about 16 mm long, while plants from the same general area (*Barker 403*), as well as collections from other localities are to 20 cm high, with tepals over 25 mm long. This variation may be seasonal but is just as likely to be genetic.

Three collections were cited by Baker (1892) in the protologue, *Drège 8478*, *Masson s.n.*, and *H. Bolus 4341*. Of these, Foster designated the Drège specimen at the Kew Herbarium the "type" and a duplicate at Geneva the "isotype." Following my practice in this revision, the Kew specimen is accepted as effectively lectotypified by Foster. Baker believed that the flowers were bright red-purple, but the type material I have

examined has the dull blackish flowers typical of several dry collections, which are known to have been deep yellow when live.

Specimens examined. SOUTH AFRICA. CAPE: 3318 (Cape Town), near Malmesbury (BC), *Schlechter 1652* (B, BR, K), *H. Bolus 4339* (K); near Wellington (DB), *Compton 11732* (NBG), *Barker 403* (NBG, STE); between Paarl and Pont, *Drège 8478* (G, K, L); Hercules Pillar (DD), *Compton 16014* (BOL, NBG); Mulders Vlei, damp sandy ground, *Lewis 4448* (SAM); N base of Joostenberg, on reddish sand, *Pillans 9262* (BOL, K); flats N of Hercules Pillar in moist places, *Leighton 555* (BOL, K); flats N of Paarl, *Leighton 2002* (BOL); flats at N end of Paarl, *Esterhuysen 6127* (BOL).

3319 (Worcester) foot of the Elandskloof Mts., near entrance to Elandsberg farm, stony ground (AC), *Goldblatt 6212* (MO); Wellington, foot of Groenberg in renosterveld (CA), *Marloth 11661* (PRE).

WITHOUT PRECISE LOCALITY: Cape of Good Hope, *Ecklon & Zeyher Irid. 217* (K), *Masson s.n.* (BM, K).

35. Geissorhiza stenosiphon Goldbl., sp. nov. TYPE: South Africa. Cape: Cold Bokkeveld Mts., Hexberg, SE slopes at ca. 4,000 ft., *Viviers 1300* (holotype, STE; isotypes, JF, K, MO, NBG, S, WAG).

Planta 10–30 cm alta, tunicis cormi concentricis pallide brunneis, foliis 3, teretis, caule erecto vel inclinato, spica 1–2 florum, bracteis 15–20 mm longis, floribus hypocrateriformibus albis, reverso carneis, tubo perianthii 40–50 mm longo, filamentis 2 mm longis, antheris 2–3 mm longis, ramis styli inter apicis tubi et basi antherarum divergentibus.

Plants slender, 10–30 cm high excluding the flowers. *Corm* globose, 9–12 mm diam., tunics light brown, concentric to more or less imbricate (? by distortion) with regular notches below, brittle-membranous to slightly woody, drawn into bristles above. *Cataphylls* usually 2, membranous, flushed purple above, the upper reaching above the ground. *Leaves* 3, the lower two basal, terete with 4 narrow longitudinal grooves, erect, reaching to about the middle of the spike, the third inserted above the ground and sheathing the stem below, also terete. *Stem* erect to inclined, unbranched, bearing an entirely sheathing, herbaceous stem bract in the upper half, this 15–22 mm long. *Spike* 1–2-flowered; *bracts* 15–20 mm long, the outer pale green with the upper margins membranous to dry, the inner entirely membranous, half to two-thirds as long as the outer. *Flowers* hypocrateriform, white, the tube and reverse of the tepals pale pink, occasionally purple, becoming darker on fading; *perianth tube* 40–50 mm long, cylindric throughout; *tepals* 12–14 mm long, lanceolate, ca. 4 mm wide, the inner somewhat larger but shorter than the outer. *Filaments* 2 mm long; *anthers* 2–3 mm long. *Ovary* 2–3 mm long, *style* reaching at least to the apex of the perianth tube, or to the top of the filaments, branches 2–2.5 mm long, ascending but becoming gently recurved ultimately. *Capsule* oval, ca. 10 mm long. *Chromosome number,* unknown.

Flowering time. December.

Distribution. Apparently restricted to the upper slopes of Hexberg in the Cold Bokkeveld Mountains.

Geissorhiza stenosiphon is included here in *Geissorhiza* with some hesitation as it has a number of features that do not conform to the normal condition for the genus. The style in the several specimens known divides between the mouth of the perianth tube and the apex of the filaments and the branches themselves are relatively long. This is reminiscent of the related genus *Hesperantha* in which the style divides either at the apex of the tube or occasionally within the tube. However, the style branches of *Hesperantha* are always very long and when exserted from the tube, as is usual, always spread horizontally (Goldblatt, 1984). The fact that the style sometimes divides well above the mouth of the tube is completely inconsistent with *Hesperantha* but does have a parallel in *Geissorhiza,* where the unrelated species, *G. spiralis* and *G. torta,* have a style that divides near the base of the anthers. Also, in two species of *Geissorhiza,* the style and style branches are entirely included in the perianth tube. Thus *G. stenosiphon* is not entirely discordant with *Geissorhiza.* Other features of *G. stenosiphon* such as the terete, four-grooved leaves, flower open during the day and the apparently extrorse anthers accord well with *Geissorhiza* and not at all with *Hesperantha.* The majority of species of the latter, including almost all white-flowered species open only in the late afternoon or evening. Moreover, the anthers in *Hesperantha* are introrse at anthesis and terete four-grooved leaves are not known in the genus.

The affinities of *Geissorhiza stenosiphon* within the genus are uncertain. The remarkably long and slender perianth tube as well as the unusual style that divides at or below the base of the anthers set the species well apart. Similar long tubes occur only in section *Engysiphon* but species of this section are otherwise very different, being more robust, and having declinate zygomorphic flowers, long floral bracts and distinctive long capsules. I assign *G. stenosiphon* tentatively to subgenus *Weihea* and to section *Angustifolia.* The

terete leaf and the apically membranous to dry bracts accord well with *G. juncea* of this section. The long perianth tube is the only character discordant with the section apart from the peculiar style that divides between the mouth of the tube and the base of the anthers. It seems reasonable to regard the long tube as a relatively recently evolved feature directly adapted to a specific pollinator.

The species was discovered only three years ago in 1982 by Elsie Esterhuysen who found a few plants at the end of the flowering season. The following year repeated visits to the Hexberg, its only known site, by Mike Viviers, Forestry Officer at Cedarberg Forest Station, resulted in the discovery of extensive populations above 1,500 m. *Geissorhiza stenosiphon* is apparently restricted to the south and east slopes of Hexberg alone where it blooms in early summer on damp south to east trending slopes at altitudes above 1,500 m.

Specimens examined. SOUTH AFRICA. CAPE: 3219 (Wuppertal) Cold Bokkeveld, near Elands Kloof, Hexberg slopes at ca. 4,000 ft. (CA), *Esterhuysen 35847* (MO); Hexberg, 1,500 m, E–W trending kloofs on S-facing slopes, in peaty soils *Viviers 1300* (JF, K, MO, NBG, S, STE, WAG).

SECTION *IXIOPSIS*

6. Section Ixiopsis Goldbl., sect. nov. TYPE: *G. hesperanthoides* Schltr.

Geissorhiza subgenus *Ixiopsis* Foster, Contr. Gray Herb. 135: 70. 1941, pro parte but excluding the type species, now *Gladiolus bojeri* (Baker) Goldbl.

Tunicae cormi molles membranaceae vel fibrosae reticulatae, foliis 2–3 linearibus marginibus costisque incrassatis, bracteis herbaceis vel membranaceis, supra saepe siccis, floribus actinomorphis, stellatis vel hypocrateriformibus, tubo brevi vel ad apicem bracteararum extenso.

Corm tunics soft and membranous to fibrous and reticulate, *leaves* 3, the upper one or two sometimes bract-like and sheathing, the margins and midrib heavily thickened, linear, *bracts* herbaceous to membranous becoming dry above, *flowers* stellate to hypocrateriform, actinomorphic, the tube either short, or reaching to the apex of, or well-exserted from the bracts, stamens equal.

Species. 5.

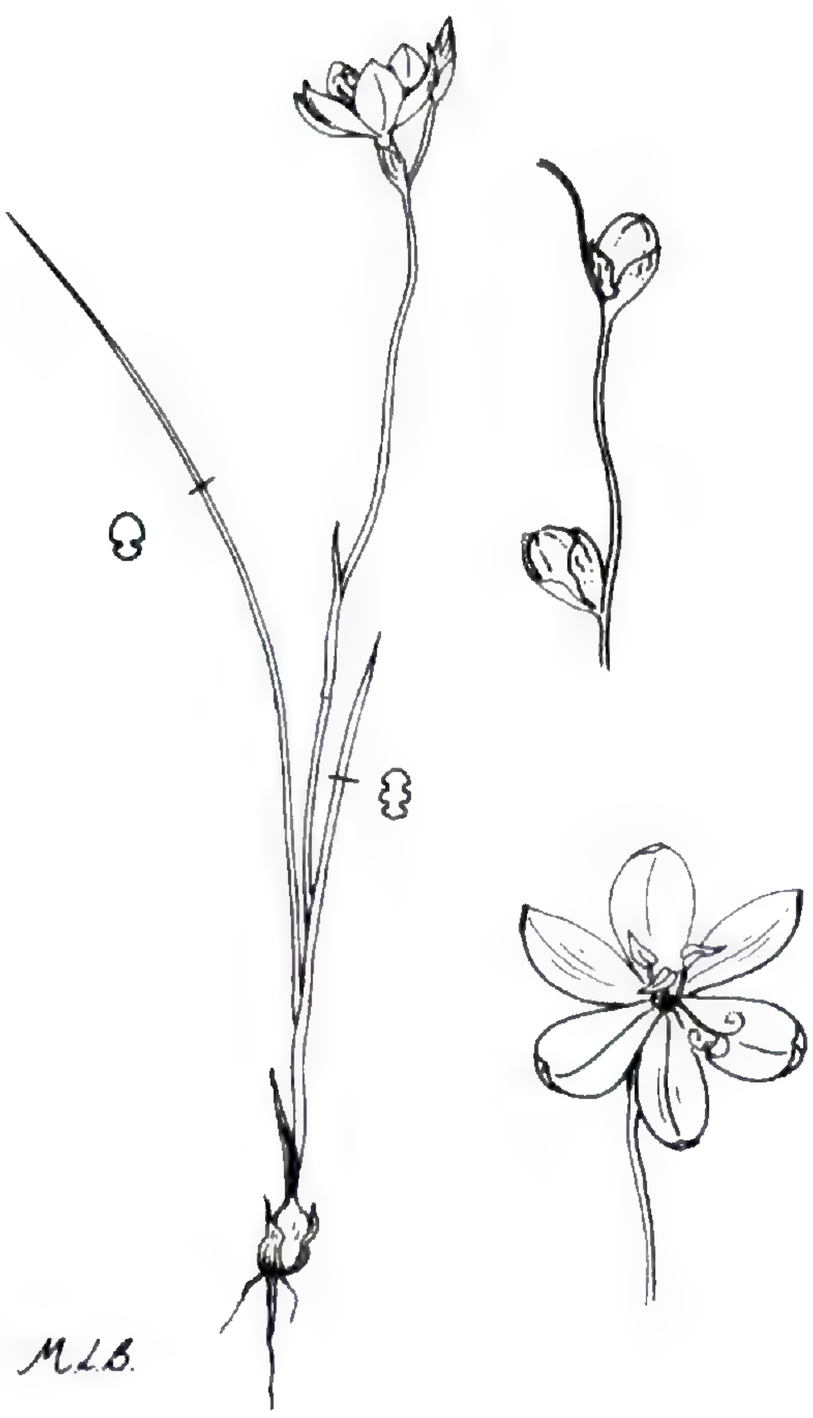
36. Geissorhiza umbrosa Lewis, J. S. African Bot. 7: 46–47. 1941. TYPE: South Africa. Cape: wet rocks on Table Mt., *Lewis 662* (lectotype, SAM 54288, here designated; isolectotypes, BOL, PRE). FIGURE 45.

Plants 12–30 cm high. *Corm* globose, 3.5–6 mm diam., the remains of older corms sometimes persisting below, tunics either membranous to soft papery and usually accumulating very little, or composed of medium to fine reticulate fibers. *Cataphyll* membranous, often brownish. *Leaves* 3, linear (to subterete), erect to falcate, 1–2 mm wide, one-third to as long as the stem, oblong in section, margins and midrib thickened and 2-grooved on each surface, the lower two basal, the second leaf shorter and sheathing the lower part of stem for a short distance (occasionally with no free apex), the uppermost leaf inserted on the lower third of the stem, sheathing for at least two-thirds to almost entirely. *Stem* erect or inclined, smooth, simple, or rarely 1-branched. *Spike* 2–4(–10)-flowered, lax; *bracts* 6–8(–10) mm long, green, or becoming dry in upper half at flowering time. *Flower* stellate, white, the reverse of the outer tepals often pink or reddish especially on fading; *perianth tube* 2.5–4 mm long; *tepals* 10–13 mm long, 5–7 mm wide, obovate. *Filaments* 4–5 mm long; *anthers* 3–4 mm long, pale yellow. *Ovary* 2–3 mm long; *style* branching near the apex of the anthers, branches ca. 1.5 mm long, recurved. *Capsule* globose, 5–6 mm long. *Chromosome number,* unknown.

Flowering time. Late October to December.

Distribution. Sheltered, damp sites in the mountains of the southwestern Cape from the Peninsula east to the Riviersonderend Mountains and north to the Cedarberg. Figure 45.

Geissorhiza umbrosa appears to be related to the fairly widespread montane and lowland *G. juncea* (section *Angustifolia*) on the one hand and to *G. hesperanthoides* and *G. alticola* (section *Ixiopsis*) on the other and it seems to be a link between these two sections. It is particularly difficult to distinguish *G. umbrosa* both vegetatively and in flower from *G. juncea,* but it is distinct in its corm which has tunics of soft, but rather irregularly broken membranous to fibrous layers. This contrasts sharply with the corm of *G. juncea* which has hard concentric layers forming bristles above. *Geissorhiza umbrosa* also has flattened rather than completely terete 4-grooved leaves that are found in *G. juncea.* In *G. umbrosa,* the leaves are slightly oblong in section, with prominently thickened midrib and margins and deep grooves between.



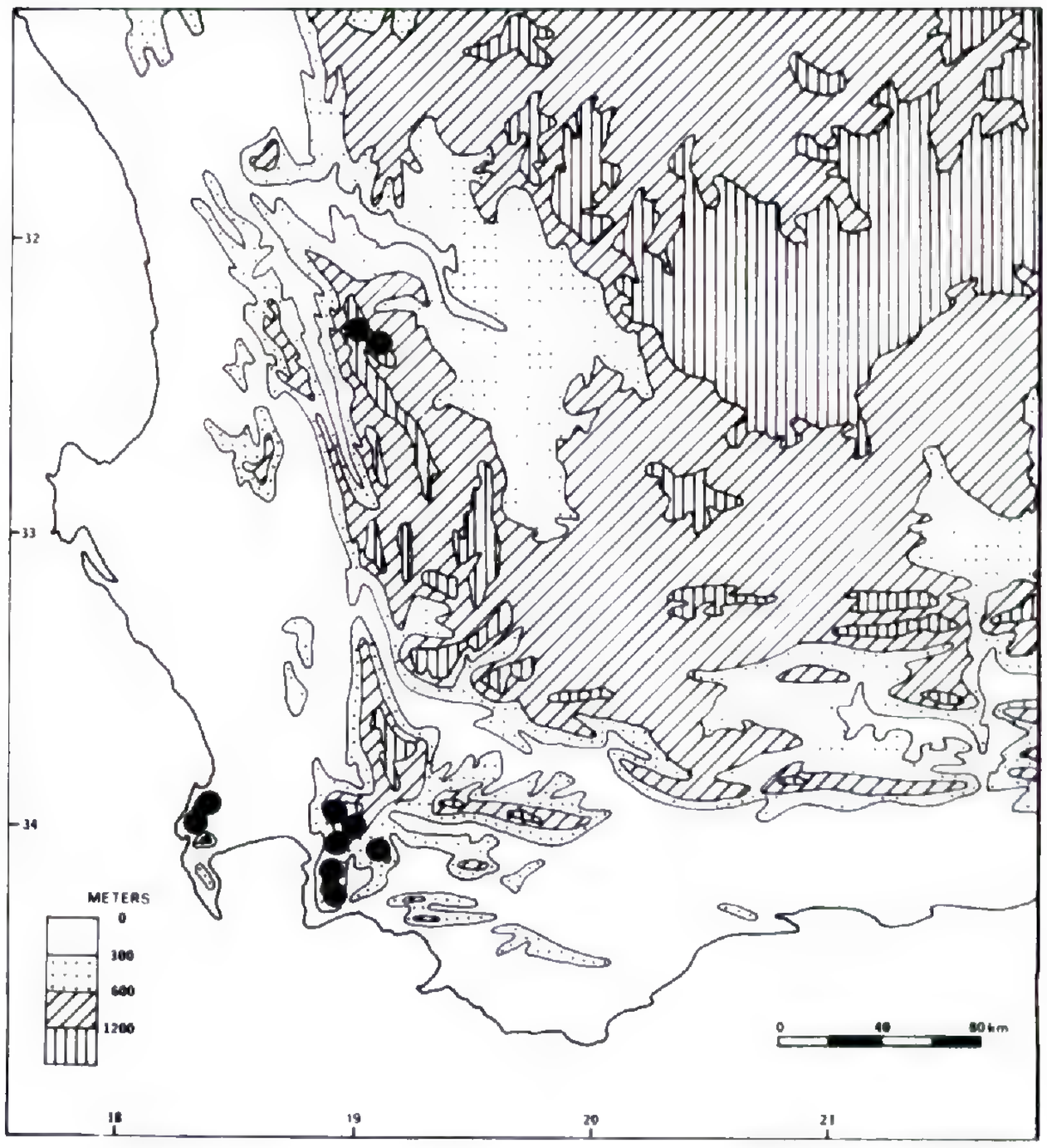


FIGURE 45. Morphology and distribution of *Geissorhiza umbrosa*. Habit ×0.5; flower and fruiting stalk life size; leaf section enlarged (*Goldblatt 6727*, Table Mt.).

Confusion of *Geissorhiza umbrosa* with *G. similis* is frequent in the absence of corms. Both species have relatively small white flowers, unbranched stems and slender leaves with thickened margins and midribs. The corm tunics of *G. similis* are hard and woody to firm-papery and distinctly imbricate. In plants that lack corms, the flowers must be measured carefully. *Geissorhiza similis* has smaller flowers with tepals 9–12 mm long, a tube 2.5–3 mm long, not exceeding the bracts and shorter filaments and anthers than those of *G. umbrosa*. Despite that close similarity of the above ground parts of the two species, they are probably only distantly related and are here placed in different subgenera.

The circumscription of *Geissorhiza umbrosa* is expanded here to include a form from the mountains east of the Cape Flats, which has corm tunics composed of medium to fine reticulate fibers and persistent older corms. Plants with fibrous corm tunics rather than the typical papery to membranous tunics, differ in no other way from typical *G. umbrosa* and cannot reasonably be regarded as belonging to separate species. A tendency for the tunics to become fibrous can be seen in some collections of the type form from the Cape Peninsula (*H. Bolus 4985*), supporting my view that forms with fibrous or membranous tunics are conspecific.

The soft tunics of *Geissorhiza umbrosa* can perhaps be correlated with its moist habitat. Species in several genera of Iridaceae which typically have hard and even woody tunics exhibit a similar tendency to have softer corm tunics in moister habitats. *Geissorhiza umbrosa* grows in cracks in cliffs, in moss on south-facing slopes or in marshes at high elevations where summer moisture is available from the prevailing southeast winds which water the higher mountains of the southwestern Cape. In these sheltered places plants flower late in the season, in November and December in the south but in the drier north, in October and November. In open or marshy places *G. umbrosa* flowers only after fires but in rocky sites it may bloom annually unless completely overgrown by surrounding vegetation.

Two collections from the Cedarberg, *Esterhuysen 35669A* and *Goldblatt 5140*, match the Table Mountain form reasonably well and are assigned to *Geissorhiza umbrosa*. Another Cedarberg collection, *Esterhuysen 35669* from the same locality as *35669A*, has broken brittle tunics and smaller flowers and corresponds closely to *G. similis*. The Cedarberg–southwestern Cape

break in distribution is unusual and may reflect lack of collecting in the area between rather than a true disjunction. *Geissorhiza umbrosa* is inconspicuous and few flowered and it may well have been overlooked in the intervening mountains.

Specimens examined. SOUTH AFRICA. CAPE: 3219 (Wuppertal) Cedarberg, Middelberg vlakte (AC), *Goldblatt 5140* (MO, NBG, PRE); South Cedarberg, path from base of Sneeuberg to the Maltese Cross, in marshy area after fire (CA), *Esterhuysen 35669A* (MO).

3318 (Cape Town) Table Mt., lower plateau (CD), *Lewis 960* (K, SAM 56481), *Goldblatt 6727* (MO, PRE); Table Mt., rock crevices in cliffs above Stinkwater, 3,000 ft., *H. Bolus 4985* (BOL); wet rocks, Table Mt., *Lewis 662* (BOL, SAM); in summo Monte tabulari, *Pappe s.n.* (SAM); summit, Table Mt., *Scott Elliot 113* (E), *Dümmer 182* (E); Echo Valley, Table Mt., *Compton 8305* (NBG); Table Mt., W slopes, 2,000 ft., *Esterhuysen 8217* (BOL); between rocks at summit of Table Mt., *Ecklon 315* (BM, G, M, MO, Z); Table Mt., lower plateau on mossy cliff in running water, *Goldblatt 5306* (MO, NBG, PRE, S); Table Mt. between Skeleton and Window Gorges, *Goldblatt 6227* (MO, PRE); Table Mt., ca. 3,200 ft., top of gully, *Esterhuysen 35386* (BOL, K, MO, US); "Waai Vley," wet rocks, *Wolley Dod 2146* (in part) (K); summit of Table Mt., *H. Bolus 4615* (BM, BOL, K); damp rocks in a kloof over Orange Kloof farm, ca. 1,200 ft., *Wolley Dod 3365* (BOL); Table Mt., 2,500 ft., *Schlechter 130* (B, FI, G, K, P, W, Z); Devils Peak, S side of summit, *Esterhuysen 35712* (MO); on precipices, Swartboskloof, Jonkershoek (DD), *Borchardt 551* (BOL).

3418 (Simonstown) Hottentots Holland, Moordenaars Kop (BB), *Stokoe s.n.* (SAM); between Somerset Sneeukop and Landrostkop, *Stokoe s.n.* (SAM 55104); Somerset Sneeukop, rock ledges, ca. 5,000 ft., *Esterhuysen 2934* (BOL), *8235* (BOL); Kogelberg, *Stokoe s.n.* (SAM 56413); NE side of Platboskop, Kogelberg Forest Reserve (BD), *Boucher 430* (STE); Platberg, *Boucher 189* (STE).

3419 (Caledon) Lebanon Forest Reserve, Jakkals River catchment Ia (AA), *Haynes 438* (STE); Schilpadkop area, Riviersonderand Mts. (BA), *Esterhuysen 21051* (BOL).

37. Geissorhiza alticola Goldbl., sp. nov. TYPE: South Africa. Cape: Louwshoek Peak, above Kaaimansgat, Villiersdorp, *Esterhuysen 35626* (holotype, MO; isotypes, BOL, K, NBG, PRE, S, WAG). FIGURE 46.

Planta 20–30 cm alta, tunicis cormi papyraceis, foliis (2–)3, inferiore basali quadrisulcato, superioribus caulem vaginantibus, caule erecto, spica 3–5 florum, floribus stellatis caeruleo-violaceis, tubo 2–3 mm longo, tepalis 11–13 mm longis, antheris 4 mm longis, capsula globosa 5–6 mm longa.

Plants 20–30 cm high. *Corm* globose, symmetric 7–10 mm diam., tunics papery, light brown, notched or torn below, the layers not accumulating. *Leaves* (2–)3, linear, 2–3 mm wide, with 2 narrow grooves on each surface, and margins and midrib much thickened, the lowermost basal, the second inserted near ground level and sheathing the lower part of the stem, apex free for a short distance, the upper leaf inserted in the mid part of the stem and sheathing almost entirely but with a short free apex. *Stem* erect, straight, unbranched. *Spike* flexuose, 3–5-flowered; *bracts* 7–10 mm long, herbaceous below, dry and membranous above. *Flowers* stellate, blue-violet; *perianth tube* short, 2–3 mm long, infundibuliform; *tepals* 11–13 mm long, obovate, ca. 5 mm wide. *Filaments* 4–5 mm long; *anthers* 4 mm long, yellow. *Ovary* 2–3 mm long, *style* dividing near the apex of the anthers, becoming declinate, branches recurved. *Capsule* globose, 5–6 mm long. *Chromosome number,* unknown.

Flowering time. December to early February.

Distribution. High altitudes, 5,000–6,000 ft. in the Du Toits Kloof-Wemmershoek-Stettynskloof Mountain complex of the southwestern Cape. Figure 46.

Geissorhiza alticola is a high altitude endemic of the southwestern Cape mountains. It has been collected on only a few occasions, always by Elsie Esterhuysen, whose exploration of the mountain flora of Southern Africa is without parallel. The species appears to be allied to the *G. hesperanthoides* complex (including as well *G. nubigena* and *G. umbrosa*), and it is similar to these species in general appearance and leaf morphology but it has unbroken, papery rather than fibrous corm tunics. It can be distinguished from other high mountain species by its very short infundibuliform perianth tube, 2–3 mm long and fairly large blue-violet flower. Normally only the lowermost leaf is produced to any extent while the two upper leaves sheath the stem for most or all of their length.

Geissorhiza alticola is evidently confined to the Du Toits Kloof-Wemmershoek-Stettynskloof Mountain complex between Worcester and Paarl. It occurs only on the higher peaks, above 5,000 ft., and blooms in mid to late summer. Adequate moisture is available at this season from the prevailing southeast winds which water only the higher mountains of the southwestern Cape while the lowlands remain dry through the summer.

FIGURE 46. Morphology and distribution of *Geissorhiza alticola*. Habit ×0.5; flower life size; partial flower and gynoecium ×2; leaf section much enlarged (*Esterhuysen 35626*, Wemmershoek Peak).

Specimens examined. SOUTH AFRICA. CAPE: 3319 (Worcester) Wemmershoek Peak, below the S summit, base of rocks (CC), *Esterhuysen 36376* (BOL, MO, PRE), *35863* (E, K, MO, NBG, PRE, S, US, WAG); S slope of ridge between Goudini Sneeukop and Deception Peak, 5,000 ft. (CD), *Esterhuysen 33445* (BOL, K, MO, PRE); Stettynsberg, summit amongst rocks, 5,900 ft., *Esterhuysen 11161* (BOL); Louwshoek Peak, above Kaaimansgat, Villiersdorp, *Esterhuysen 35626* (BOL, K, MO, NBG, PRE, S, WAG).

38. Geissorhiza hesperanthoides Schltr., Bot. Jahrb. Syst. 27: 97. 1899; Foster, Contr. Gray

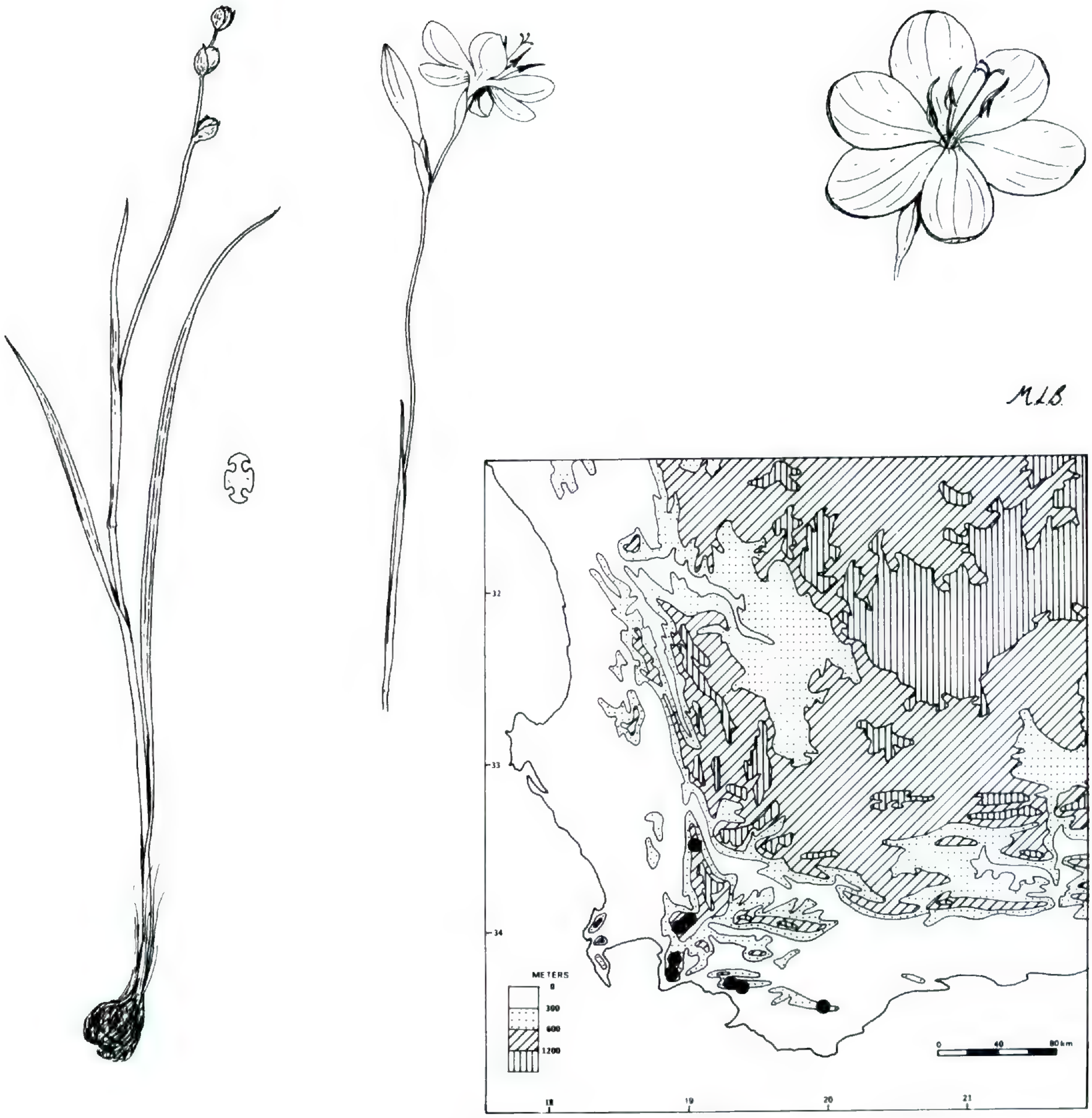


FIGURE 47. Morphology and distribution of *Geissorhiza hesperanthoides*. Habit and flowering stalk ×0.5; flower life size; leaf section much enlarged (*Esterhuysen 35381*, Victoria Peak).

Herb. 135: 73. 1941. TYPE: South Africa. Cape: summit of mts. near Vogelgat, *Schlechter 9555* (lectotype, B, here designated; isolectotypes, B, BM, G, K, MO, PH, PRE, Z). FIGURE 47.

Plants 15–30 cm high. *Corm* globose, flattened below, 5–7 mm diam., tunics of fine, pale reticulate fibers, sometimes with papery, fragmented layers between, fibers extending upwards in a neck. *Cataphyll* membranous, becoming fibrous below or not evident. *Leaves* 3, rarely 2, linear, 2–3 mm wide, the margins and midrib much thickened and with 2 narrow grooves on each surface, occasionally sticky with adhering sand, the lowermost leaf basal, longest, the second inserted near ground level and sheathing the lower part of the stem for a short distance, the uppermost inserted in the middle part of the stem and sometimes sheathing entirely or with a short free apex. *Stem* more or less erect to inclined, very rarely branched. *Spike* flexuose, 1–3-flowered; *bracts* ca. 10 mm long, herbaceous, reddish above, often with hyaline apices, the inner shorter and narrower than the outer. *Flower* stellate, tepals slightly cupped, blue to violet; *perianth tube* 5–8(–10) mm long, almost reaching the apex of the bracts at anthesis, becoming shortly exserted in

old flowers; *tepals* 12–18 mm long, oblanceolate, 6–8 mm wide. *Filaments* 7–10 mm long; *anthers* 4–5 mm long, yellow. *Ovary* 2–3 mm long, *style* exceeding the stamens, declinate, branches ca. 3 mm long, recurved. *Capsule* globose, ca. 6 mm long. *Chromosome number,* unknown.

Flowering time. Late November to December (January at highest elevations).

Distribution. Mountains of the southwestern Cape from Wellington Sneeukop and Victoria Peak south to the Bredasdorp Mountains, at middle to upper altitudes usually in damp sites. Figure 47.

Geissorhiza hesperanthoides is unusual in *Geissorhiza* in having fine, fibrous corm tunics, a characteristic shared only by *G. nubigena* and *G. umbrosa.* Fibrous corm tunics are a specialized and derived character in *Geissorhiza,* where hard woody concentric tunics are most likely the primitive state, and *G. hesperanthoides* and its allies comprise a specialized group in the genus. *Geissorhiza hesperanthoides* is closely allied to *G. nubigena,* also a mountain species, which has until now been included in *G. hesperanthoides.* The two are similar in vegetative morphology but have different flowers. Those of *G. hesperanthoides* have somewhat cupped, broad, violet blue tepals and a perianth tube 5–8 mm long, extending to 7–10 mm in older flowers, typically not or barely exserted from the bracts. In *G. nubigena,* the pink flowers have narrower tepals that extend at right angles to the tube which is 10–18 mm long, well exserted at anthesis and becoming even longer in older flowers. Differences between the two species are discussed in more detail under *G. nubigena,* number 40 in this treatment.

Geissorhiza hesperanthoides occurs in Cape mountain vegetation in semi-marshy conditions at mid to upper elevations. It is not rare, but it blooms irregularly and is conspicuous only in the seasons following a fire or in cleared areas where it is not completely overgrown by the dominant shrubby vegetation. It extends from the Bains Kloof Mountains and Victoria Peak in the north, through the Hottentots Holland Mountains and Kogelberg to the Klein River and Bredasdorp Mountains. Although apparently disjunct between Kogelberg and the Klein River and Bredasdorp Mountains, it probably occurs in suitable habitats in the intervening mountains. The collections from Upper Wellington Sneeukop in the Bains Kloof Mountains seem somewhat unusual. The tunics are papery with no apparent development of fibers with age. The perianth tube in these populations is also somewhat longer than usual for *G. hesperanthoides* being in the 8–10 mm range, which is the upper limit for the species.

Specimens examined. SOUTH AFRICA. CAPE: 3318 (Cape Town) Jonkershoek Forest Reserve (DD), *Rycroft 1464* (SAM).

3319 (Worcester) Upper Wellington Sneeukop, steep S slopes and ledges, 5,500 ft. (CA), *Esterhuysen 33073* (BOL, K, MO); Upper Wellington Sneeukop, base of small cliffs in lower shale band, 5,000 ft., *Esterhuysen 34501* (BOL).

3418 (Simonstown) SE slopes of Kogelberg, 3,000 ft. (BB), *Esterhuysen 13328* (BOL, PRE); Landdrostkop, Caledon Division, *Stokoe 8094* (BOL).

3419 (Caledon) Victoria Peak, 3,500–4,500 ft. (AA), *Esterhuysen 9769* (BOL); Victoria Peak, base of high cliffs, *Esterhuysen 33111A* (BOL); Victoria Peak, Jonkershoek Mts., *Esterhuysen 35381* (MO), *35870* (E, K, MO, NBG, PRE, S, US, WAG), *Kerfoot 6194* (NBG); Groenland Mts., Mt. Lebanon, 3,800 ft., damp moss on S slope, *Goldblatt 6914* (MO); Vogelgat, above Hermanus (AD), *Schlechter 9555* (B, BM, G, K, MO, PH, PRE, Z), *Goldblatt 5397* (K, MO, NBG); Vogelgat, 1,600 ft., Vulture Stream gorge, *Goldblatt 5346* (MO); Vogelgat, near Beaconhead stream, *Williams 2955* (MO); mts. near Klein River Lake, *Guthrie s.n.* (BOL); summit of Aasvogelkop, Hermanus, *Jackson s.n.* (NBG 121217); top of Zoutmelkskop, Bredasdorp Mts. (DB), *Galpin 11334* (K, PRE).

39. Geissorhiza cataractarum Goldbl., sp. nov. TYPE: South Africa. Cape: above Bettys Bay, dripping S-facing cliffs in moss, *Goldblatt 5355* (holotype, MO; isotypes, BR, E, K, NBG, NSW, PRE, S, US, WAG). FIGURE 48.

Planta 10–20(–30) cm alta, cormo elongato-globoso, 4–5 mm diam., tunicis membranaceis, evanescentibus, foliis 3, inferioribus duabus basalibus linearibus, caule decumbente, spica 1–5 floribus, bracteis herbaceis, floribus stellatis, caeruleis, tubo 4–6 mm longo, tepalis 14–20 mm longis, filamentis aequalibus ca. 10 mm longis, antheris 3(–4) mm longis.

Plants 10–20(–30) cm high, often decumbent. *Corm* elongate-globose, symmetric, 4–5 mm diam., tunics pale to light brown, firm to soft membranous, not normally accumulating. *Cataphyll* membranous, usually lacking in dry specimens. *Leaves* 3, linear, 1–1.5 mm wide, margins and midrib enlarged and 2-grooved on each surface, the lower two leaves basal, usually long, curved and trailing, the uppermost leaf inserted in the lower part of the stem, short and partly sheathing. *Stem* decumbent or suberect, unbranched. *Spike* 1–5-flowered; *bracts* herba-

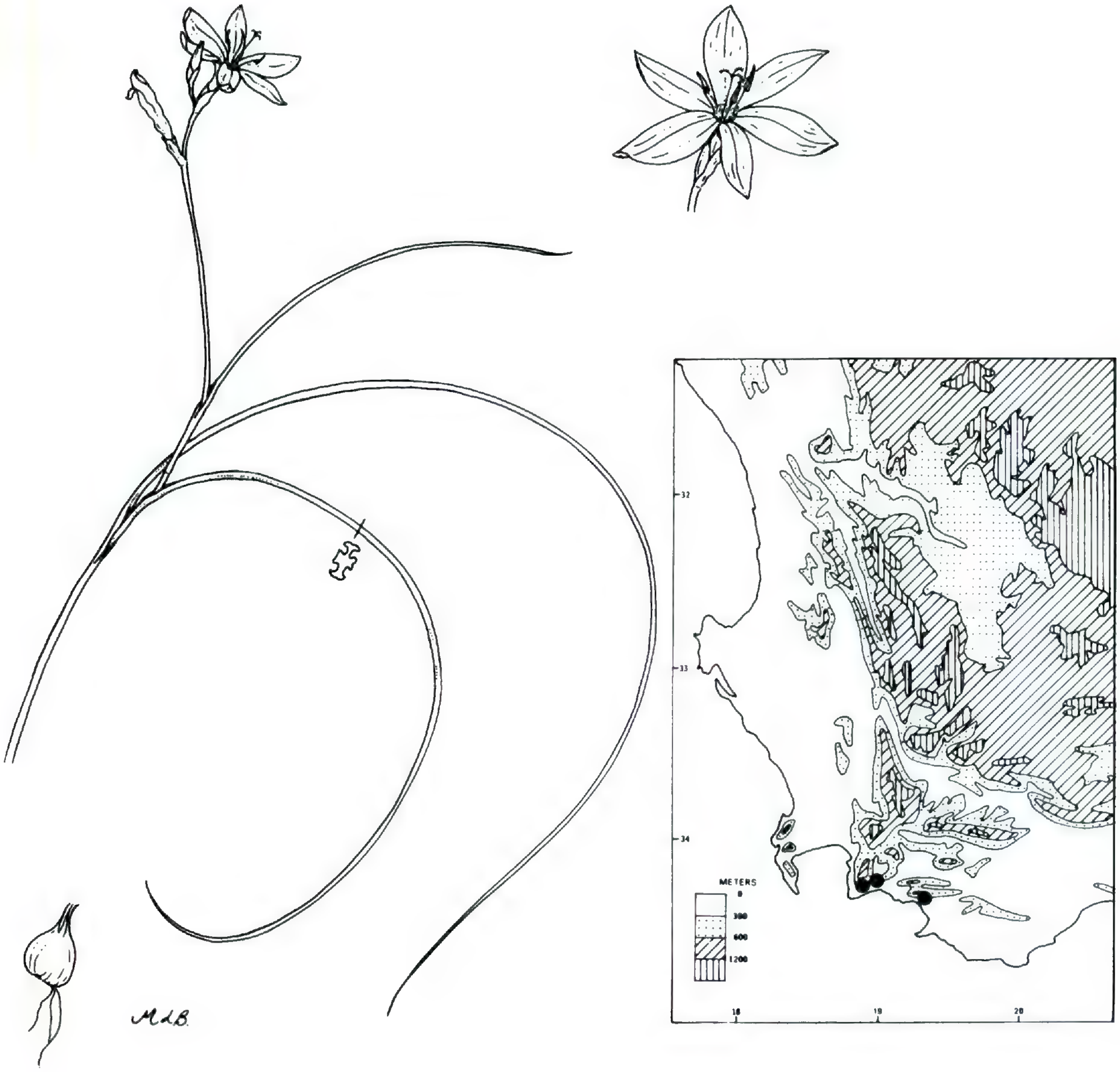


FIGURE 48. Morphology and distribution of *Geissorhiza cataractarum*. Habit ×0.5; flower and corm life size; leaf section much enlarged (*Goldblatt 5355*, waterfall at Bettys Bay).

ceous, 6–9 mm long, the upper margin membranous. *Flower* stellate, pale blue-mauve, with a white center; *perianth tube* 4–6 mm long, usually reaching to about the apex of the bracts or slightly shorter; *tepals* 14–20 mm long, elliptic, 6–8 mm wide. *Filaments* 10 mm long; *anthers* 3(–4) mm long. *Ovary* ca. 2 mm long; *style* dividing near the apex of the anthers, branches recurved. *Capsule* unknown. *Chromosome number*, $2n = 26$ (*Goldblatt 5355*).

Flowering time. Late November to mid-January.

Distribution. Wet, dripping south-facing cliffs and waterfalls in the mountains between Bettys Bay and Hermanus. Figure 48.

Geissorhiza cataractarum has a restricted distribution, occurring in isolated sites along an approximately 40 kilometer stretch of mountains, on the coast between Bettys Bay and Hermanus. It is a late flowering species, blooming in summer, from December until mid-January. Plants grow in damp moss on continually moist and dripping, south-facing cliffs that remain wet even during the dry Cape summer, an unusual habitat for *Geissorhiza*. This niche is shared with the red-flowered orchid, *Disa uniflora*, the rare,

monotypic *Unigenes* (Campanulaceae) and a few other small moisture and shade-loving plants. *Geissorhiza cataractarum* is apparently related to the *G. umbrosa–G. hesperanthoides* alliance and is assigned to section *Ixiopsis*. It is unusual in its habitat and in its particularly delicate corm tunics, that are distinctive even for the section where membranous to fibrous tunics are characteristic. The tunics of *G. cataractarum* seldom accumulate as they do in other species, but decay entirely within a year. Only occasionally can the remains of old tunics be seen in herbarium collections.

In the Klein River Mountains around Hermanus in the east of its range, a second species, *Geissorhiza bryicola* (subgenus *Geissorhiza*) occurs in similar habitats, together with *G. cataractarum, G. bryicola* flowering from October to November and *G. cataractarum* from December to January. *Geissorhiza bryicola* has small white flowers with unequal stamens, persistent, brown imbricate corm tunics and a nearly plane leaf. The two are unlikely to be confused and despite their similar habitat, are believed to be unrelated, and are assigned to different subgenera.

Specimens examined. SOUTH AFRICA. CAPE: 3428 (Simonstown) Platteberg, 2,000 ft., in moss (BD), *Stokoe s.n.* (BOL 31908, SAM 58006); kloof near Bettys Bay, *Rourke s.n.* (NBG 60746); waterfall, near Bettys Bay, *Loubser 921* (NBG); Bettys Bay, dripping cliffs, ca. 1,000 ft., in moss, *Goldblatt 5355* (BOL, BR, E, K, NBG, NSW, P, PRE, S, US, WAG).

3419 (Caledon) Palmiet River Mts. (AC), *Stokoe 920* (PRE), *Stokoe s.n.* (BOL 17519); Vogelgat Nature Reserve, Secret Falls, mossy banks on waterfall in mist spray (AD), *Williams 3404* (MO).

40. Geissorhiza nubigena Goldbl., sp. nov. TYPE: South Africa. Cape: S slopes of Victoria Peak, *Goldblatt 6827* (holotype, MO; isotypes, K, NBG, PRE, S, US, WAG). FIGURES 5, 49.

Planta 15–30 cm alta, tunicis cormi fibrosis reticulatis, foliis 3, inferioribus duobus linearibus quadrisulcatis, superiore vaginanti, caule erecto, spica 1–5 floribus, floribus hypocrateriformibus roseis, tubo 10–18 mm longo, tepalis 17–22 mm longis, antheris 5–6 mm longis.

Plants 15–30 cm high. *Corm* globose, flattened below, 5–9 mm diam., tunics of fine, pale reticulate fibers, sometimes with papery, fragmented layers between, fibers usually extending upwards in a neck. *Cataphyll* membranous, becoming fibrous below or not evident. *Leaves* 3 (rarely 2), linear, 2–3 mm wide, the margins and midrib much thickened and with 2 narrow grooves on each surface, the lowermost leaf basal, the second inserted near ground level, sheathing the lower part of the stem for a short distance, the uppermost leaf inserted in the middle part of the stem and sometimes sheathing entirely or with a short free apex. *Stem* more or less erect, very rarely branched. *Spike* flexuose, 1–5-flowered; *bracts* ca. 10 mm long, herbaceous, reddish above, often with hyaline apices, the inner shorter and narrower than the outer. *Flower* hypocrateriform, facing to one side, the tepals extended at right angles to the tube, rose pink; *perianth tube* 10–18 mm long, cylindric, reaching beyond apex of bracts on opening and becoming well-exserted; *tepals* 17–22 mm long, oblanceolate, to 9 mm wide. *Filaments* 8–12 mm long; *anthers* 5–6 mm long, yellow. *Ovary* 2–3 mm long, *style* exceeding the stamens, becoming declinate, branches 3–4 mm long, recurved. *Capsule* unknown. *Chromosome number,* unknown.

Flowering time. January.

Distribution. Middle to upper altitudes in the Hottentots Holland and Kogelberg Mountains. Figure 49.

Geissorhiza nubigena is clearly allied to the more widespread montane *G. hesperanthoides,* and it has the unusual fibrous corm tunics of this species. It has until now usually been included in this species. It is, however, not only larger in most respects than *G. hesperanthoides,* but particularly so in its perianth tube which is some 10–18 mm long and at anthesis well-exserted from the bracts. In contrast, the perianth tube of *G. hesperanthoides* is only 5–8 mm long at anthesis, extending to 7–10 mm in older flowers and typically not or barely exserted from the bracts. The flowers apparently also differ significantly. Those of *G. nubigena* are rose pink and have tepals 17–22 mm long and to 9 mm wide and extend at right angles to the tube, while in *G. hesperanthoides* the flowers are blue-violet and the tepals are 12–20 mm long, to 8 mm wide and typically somewhat cupped and relatively broader.

The range of *Geissorhiza nubigena* is completely within that of *G. hesperanthoides.* It extends from Kogelberg through the Hottentots Holland Mountains to Victoria Peak. *Geissorhiza hesperanthoides* occurs throughout this area, but extends to the north and to the southeast, through the Klein River and Bredasdorp Mountains. *Geissorhiza nubigena* appears to favor somewhat drier, better drained situations than *G. hesperanthoides* which usually grows in semi-marshy places.

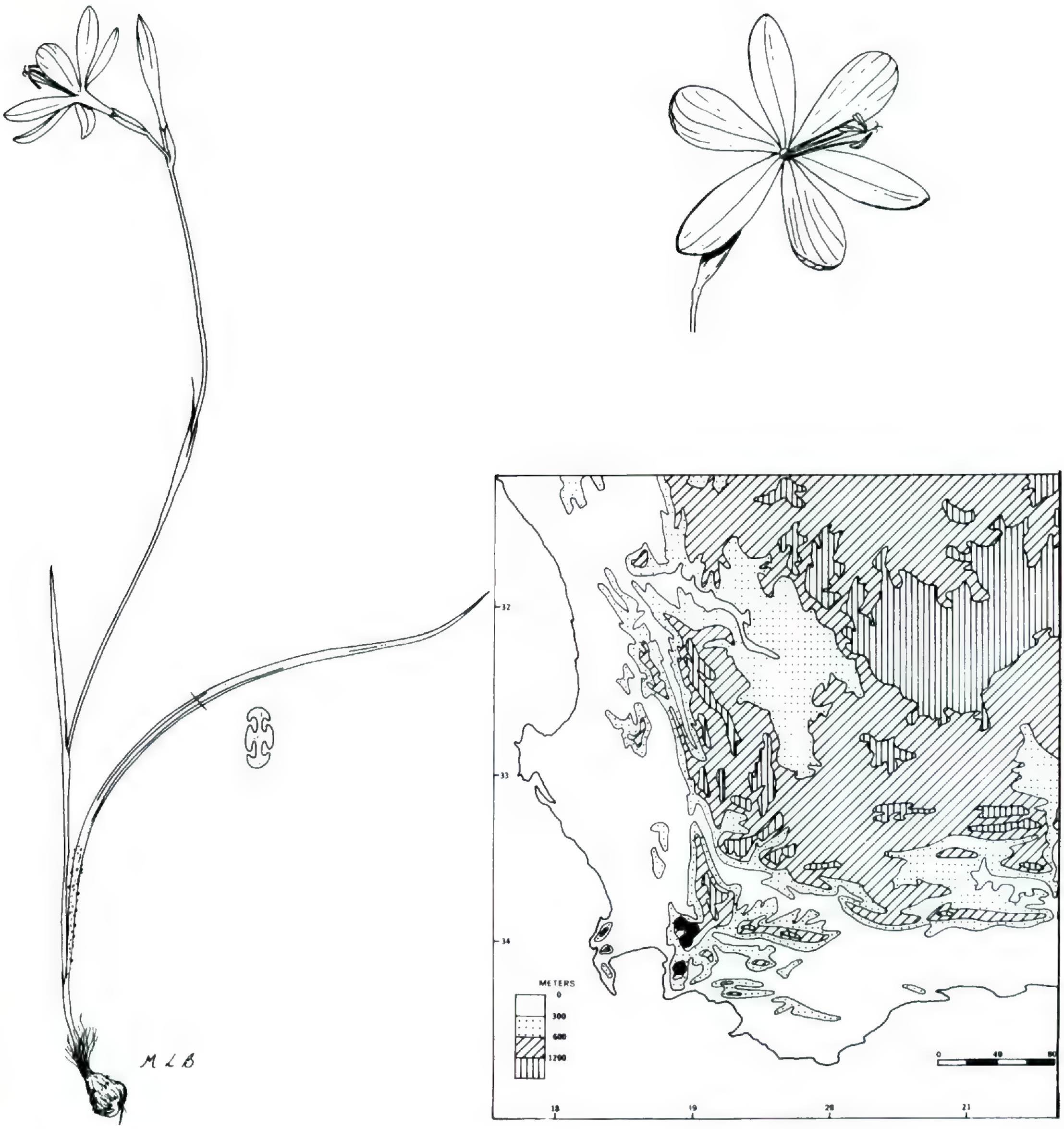


FIGURE 49. Morphology and distribution of *Geissorhiza nubigena*. Habit ×0.5; flower life size; leaf section much enlarged (*Goldblatt 6827*, Victoria Peak).

Specimens examined. SOUTH AFRICA. CAPE: 3318 (Cape Town) Jonkershoek (DD), *Rycroft 1482* (SAM).

3418 (Simonstown) Kogelberg, upper S slopes, 3,500–4,000 ft. (BB), *Esterhuysen 33120A* (BOL, MO); Kogelberg, Five Beacon Ridge, 3,000–3,500 ft., *Esterhuysen 9993* (BOL); Kogelberg, 900 m, *Boucher 2053* (PRE, STE); Hottentots Holland, N of Somerset Sneeukop, shady cliffs, 3,500 ft., *Esterhuysen 9723* (BOL, K); Sneeukop, Hottentots Holland Mts., *Begley s.n.* (SAM 10363); head of Landdrost Kloof, old fire trace, ca. 4,000 ft., *Esterhuysen 32559* (BOL); Steenbras Peak, Kogelberg State Forest, *Boucher 2791* (STE), *2718* (PRE).

3419 (Caledon) Victoria Peak, steep rocky upper slopes and on marshy sites on approach to peak, ca. 4,500 ft. (AA), *Esterhuysen 33080* (BOL); Victoria Peak, 4,500 ft., *Esterhuysen 14376* (BOL), *33111* (BOL); Victoria Peak, 5,100 ft., at foot of shale band, *Haynes & Kruger 755* (STE); E slopes of Victoria Peak, *Goldblatt 6827* (K, MO, NBG, PRE, S, US, WAG).

SECTION *ENGYSIPHON*

7. Section **Engysiphon** (Lewis) Goldbl., stat. nov. *Engysiphon* Lewis, J. S. African Bot. 7: 19–24. 1941. LECTOTYPE: *G. exscapa* (Thunb.) Goldbl.

Acidanthera Hochst. sensu Baker, Fl. Cap. 6: 130–134. 1896, pro parte.

Corm tunics hard, woody, *leaves* ensiform to

linear, either with heavily thickened margins and midrib, or with the margins raised and winged and curving around the poorly thickened midrib and nearly terete, *spike* few to several flowered, *bracts* herbaceous, the inner membranous and usually less than half as long as the outer, *flower* declinate, the tube long to very long, reaching to or well exceeding the apex of the bracts, stamens equal.

Species. 7.

41. Geissorhiza brevituba (Lewis) Goldbl., comb. nov. *Engysiphon brevitubus* Lewis, J. S. African Bot. 7: 24. 1941. TYPE: South Africa. Cape: top of Piketberg Mt., *H. Bolus s.n.* (lectotype, BOL 13651, here designated; isolectotypes, BM, K, PRE). FIGURE 50.

Plants 12–20 cm high. *Corm* globose, 15(–20) mm diam., tunics dark brown, concentric, layers fragmenting irregularly, segments drawn into short points above. *Cataphyll* pale, membranous, apparently solitary. *Leaves* usually 3, linear to narrowly ensiform, sticky on the sheath and lamina, and with sand adhering, the margins expanded at right angles to the blade, the midrib also enlarged and winged, the blade thus broadly 2-grooved on each surface, the lowermost leaf basal, largest, as long or slightly exceeding the spike, the other leaves short, becoming bract-like and sheathing for half their length, the lower of these basal or sub-basal, the upper inserted in the middle part of the stem. *Stem* erect, flexed above the sheath of the uppermost leaf and at the base of the spike, usually unbranched. *Spike* 1–3-flowered, flexuose; *bracts* 15–20 mm long, herbaceous, the inner membranous, shorter than the outer, ca. 12 mm long. *Flower* zygomorphic, stamens and style declinate, deep pink with darker veins; *perianth tube* ca. 8 mm long, not exserted from the bracts, widening towards the throat; *tepals* 25–30 mm long, 9–11(–13) mm wide, the outer wider and shorter than the inner. *Filaments* unilateral and declinate, held above the lowermost tepal; *anthers* unilateral, ca. 6.5 mm long. *Ovary* 3–4 mm long, *style* declinate, curved under the filaments, dividing near the apex of the anthers, branches ca. 4 mm long, ultimately recurved. *Capsule* unknown. *Chromosome number*, $2n = 26$ (*Goldblatt 204*).

Flowering time. September.

Distribution. Stony mountain soil in low fynbos, Piketberg Mountains. Figure 50.

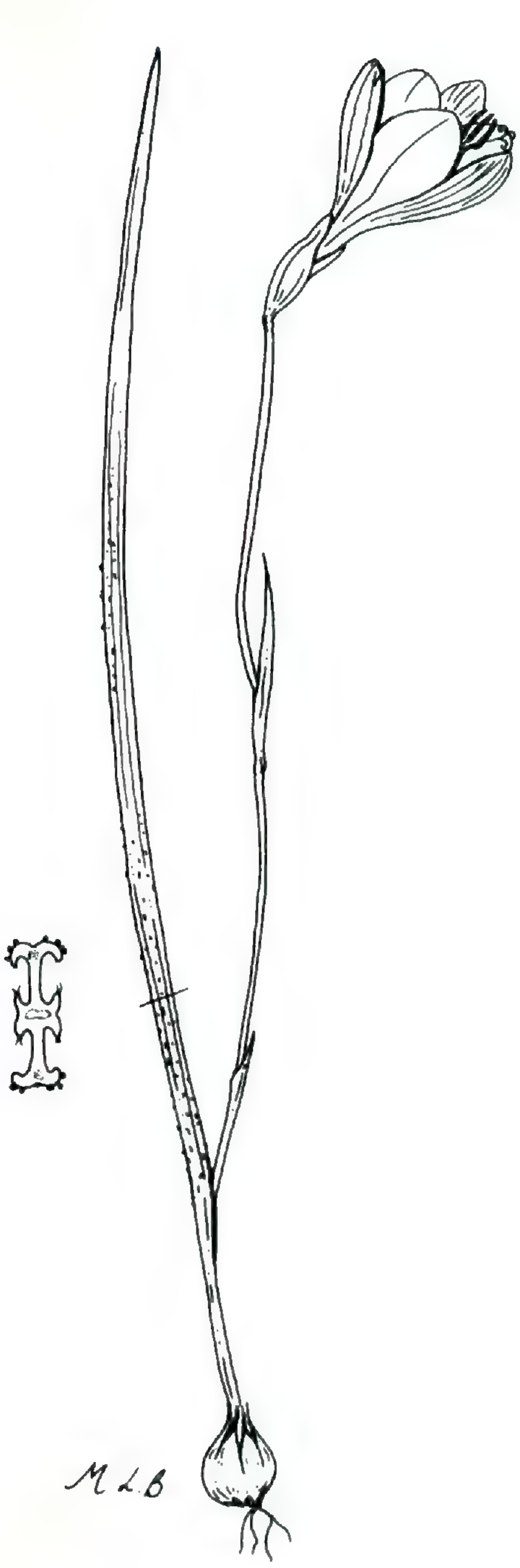
Geissorhiza brevituba is distinctive in section *Engysiphon*, in having a relatively short perianth tube, some 8 mm long, substantially shorter than the floral bracts. The bracts themselves are also relatively short for the alliance, being 15–20 mm long while the inner bract is not as short as in the other species of the section. In its other characteristics it is typical of the section having a zygomorphic flower with declinate stamens and style, the peculiar tepals with darker veins, and the single well-developed leaf with thickened and sticky margins and midrib. It is apparently most closely allied to *G. schinzii*, a species that occurs in the Caledon district, well to the southeast. This species also has a relatively short tube, some 24–32 mm long and about as long as the bracts, as well as quite broad tepals. Lewis (1941) suggested that *G. brevituba* with its short perianth tube may be closest to the ancestral type of *Engysiphon*, and it clearly has a combination of primitive features of the section. *Geissorhiza brevituba* has a very restricted distribution, having been recorded only from the Piketberg Mountains of the western Cape. It is relatively common here and is especially abundant after the veld has been burned the previous summer or autumn.

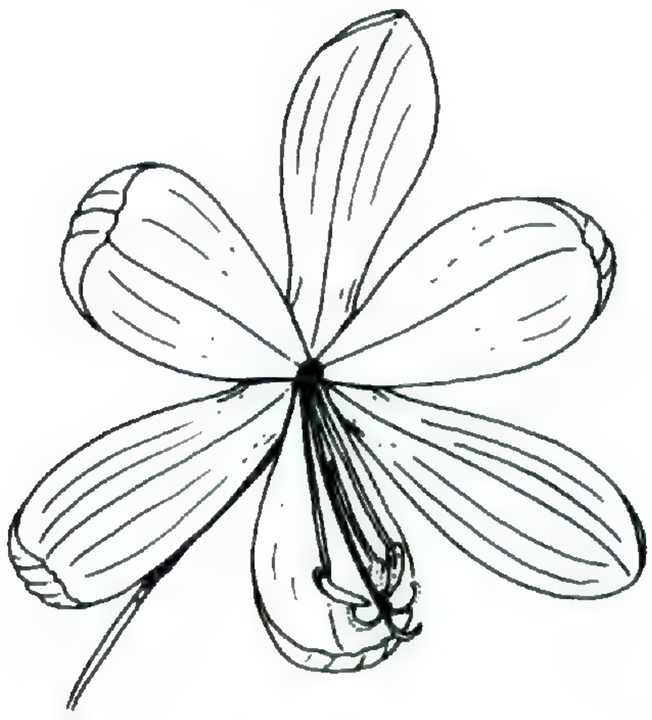
Specimens examined. SOUTH AFRICA. CAPE: 3218 (Clanwilliam) farm Waboom, slopes of Zebrakop (DB), *Taylor 5339A* (STE); top of Piketberg Mt. (AC), *H. Bolus s.n.* (BM, BOL 13651, PRE), *Barker 6713* (NBG), *Martin 855* (NBG), *1053* (NBG), *Lewis 6215* (MO, NBG), *Goldblatt 204* (BOL), *De Vos s.n.* (STE); Piketberg, *Guthrie 2705* (BOL).

42. Geissorhiza schinzii (Baker) Goldbl., comb. nov. *Acidanthera schinzii* Baker, Kew Bull. 1906: 27. 1906. *Engysiphon schinzii* (Baker) Lewis, J. S. African Bot. 7: 22. 1941. TYPE: South Africa. Cape: Houw Hoek, *Penther 587* (lectotype, Z, here designated; isolectotype, K). FIGURE 51.

Gladiolus costatus Ecklon, Topogr. Verz. Pflanzensamml. Ecklon 38. 1827 et ms., nom. nud.

Plants (10–)12–20 cm high. *Corm* globose, asymmetric, flattened below on one side, 12–18 mm diam., tunics concentric, dark brown, fragmenting irregularly, segments drawn into 15 mm long cusps above. *Cataphyll* membranous, pale, evidently solitary. *Leaves* usually 3, erect to falcate, 4–6 mm wide, sticky below and on the margins and midrib and usually with sand adhering, the margins enlarged and extending at right angles to lamina, the midrib also enlarged and





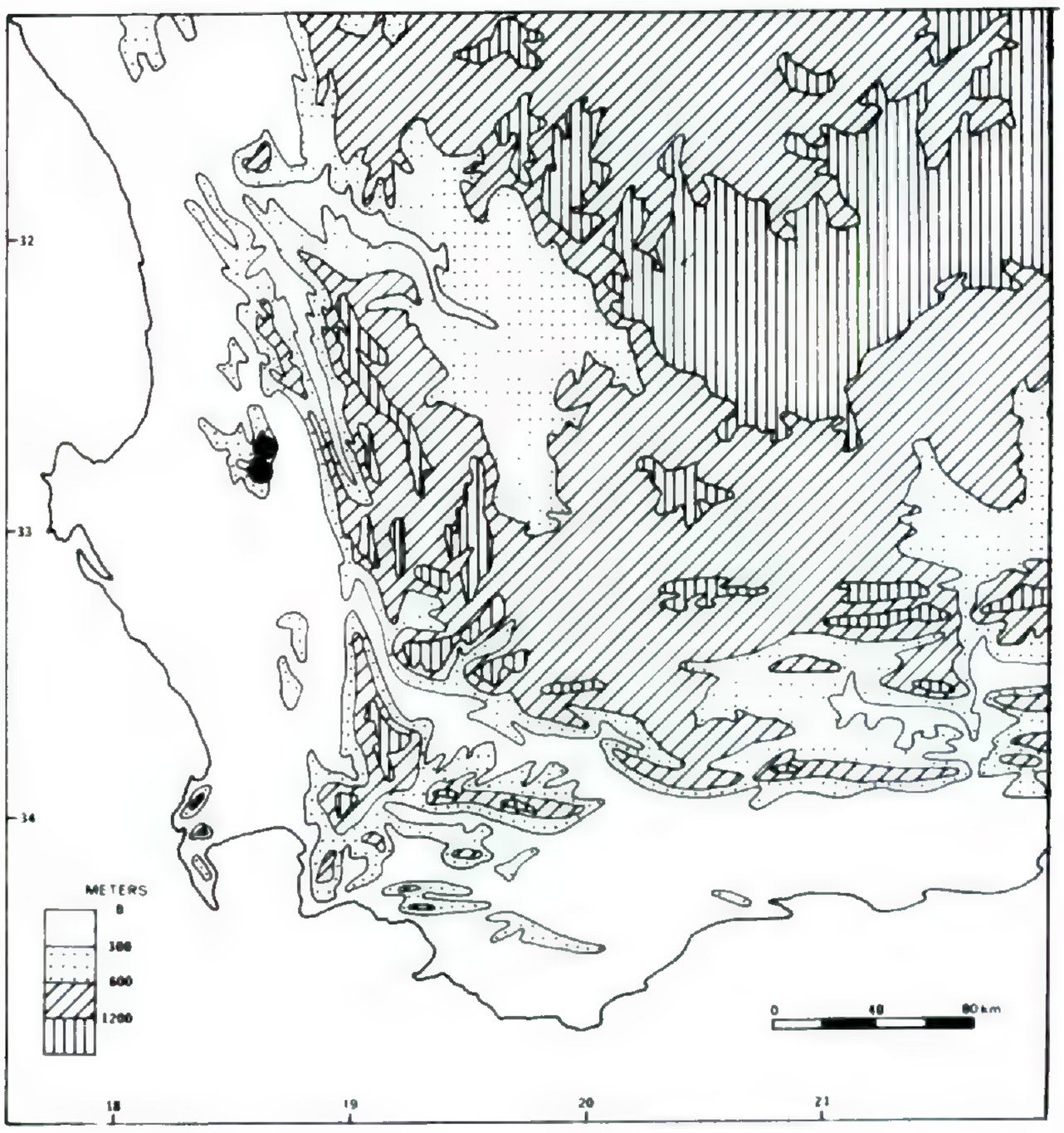


FIGURE 50. Morphology and distribution of *Geissorhiza brevituba*. Habit ×0.5; flower life size; leaf section much enlarged (*Goldblatt s.n.* no voucher, Piketberg Mts.).

winged and thus the blade with 2 wide grooves running the length of each surface, the lowermost largest, usually slightly longer than the spike, the second leaf basal or sub-basal, short, the third inserted in the mid part of the stem, both sheathing for about half their length. *Stem* inclined, flexed above the sheaths of the two upper leaves, unbranched. *Spike* 1–4-flowered, flexuose; *outer bracts* (20–)25–40 mm long, herbaceous, the inner much shorter and concealed by the outer. *Flower* zygomorphic, with the stamens and style declinate, tepals pink with darker veins; *perianth tube* 24–32 mm long, cylindric, usually emerging shortly from or occasionally somewhat shorter than the bracts; *tepals* 35–40 mm long, unequal, 9–15 mm wide, the outer shorter and broader than the inner. *Filaments* ca. 20 mm long, unilateral and declinate, held above the lowermost tepal; *anthers* 6–7 mm long, unilateral, horizontal. *Ovary* 5–6 mm long, *style* declinate, curved under the filaments, dividing near or beyond the apex of the anthers, branches ca. 3.5 mm long, ultimately recurved. *Capsule* unknown. *Chromosome number,* unknown.

Flowering time. Late August to early October.

Distribution. Caledon district, mainly montane, in sandy soils. Figure 51.

Geissorhiza schinzii is common throughout the

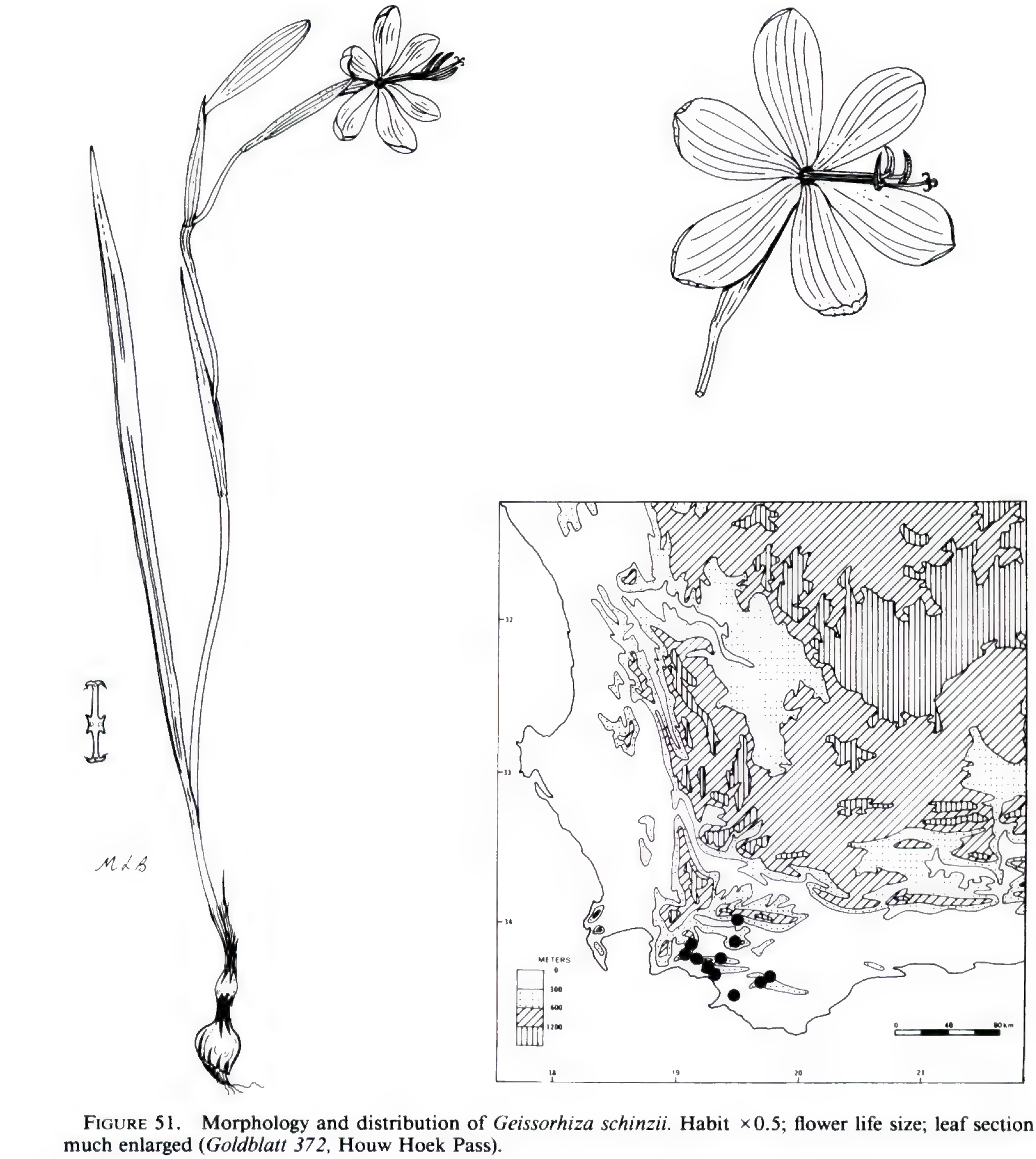


FIGURE 51. Morphology and distribution of *Geissorhiza schinzii*. Habit ×0.5; flower life size; leaf section much enlarged (*Goldblatt 372*, Houw Hoek Pass).

Caledon district, where it occurs in stony sandstone derived soil in the mountains and along the coast. It blooms well only after a veld fire the previous summer but can sometimes be seen in low fynbos in unburned vegetation. The large pink, delicately veined flowers with relatively broad tepals are distinctive, and *G. schinzii* should not be confused with other species of section *Engysiphon*. It is sometimes difficult to distinguish from *G. confusa* (*Engysiphon exscapus* sensu Lewis), but this species has cream to pale yellow flowers, a typically longer perianth tube, and proportionately narrower tepals that are usually shorter than the tube, whereas the tepals of *G. schinzii* are broad and as long or a little longer than the perianth tube.

Specimens examined. SOUTH AFRICA. CAPE: 3419 (Caledon) Houw Hoek (AA), *Thorne s.n.* (NBG 62250),

Gillett 897 (STE), *Lewis 1498* (SAM), *Werdermann & Oberdieck 158* (B, K, PRE), *van Niekerk 644* (BOL, K, PRE); Houw Hoek Pass, *Mauve 4604* (PRE, STE), *Salter 4875* (BM, K), *Goldblatt 372* (BOL), *3019* (MO); Bot River Pass, *Compton 18519* (NBG); Zwartberg, Caledon (AB), *Pappe s.n.* (BM, SAM), *Zeyher 1607* (BM, SAM); hills between Bot River and Hawston (AC), *Barker 8789* (NBG); Honingklip farm, near Bot River, *Barker 10509* (NBG); Shaws Pass (AD), *Lewis 6096* (NBG, STE), *Thompson 980* (K, PRE, STE), *Gillett 4197* (BOL, K); Shaws Mt., *H. Bolus s.n.* (BOL 22562, PRE), *Barker 9* (BOL, K); on road to Hemel-en-Aarde from Hermanus, *Gillett 46* (BOL, STE); Fern Kloof Nature Reserve, *Schmidt 29* (STE); Rotary Drive, Hermanus, *Goldblatt 3008* (MO, PRE); Genadendal (BA), *Prior s.n.* (K); Keeromskloof, Salmonsdam Nature Reserve (BC), *Hugo 2627* (STE); Fairfield (BD), *Thomas s.n.* (NBG); Baardscheerdersbos, between Elim and Gansbaai (DA), *Stokoe s.n.* (SAM 59825).

43. Geissorhiza longifolia (Lewis) Goldbl., comb. nov. *Engysiphon longifolius* Lewis, J. S. African Bot. 7: 23. 1941. TYPE: South Africa. Cape: Clanwilliam, Nieuwoudt Pass, *Leighton s.n.* (holotype, BOL 22558). FIGURES 6, 52.

Gladiolus costatus Ecklon ms. (*Ecklon & Zeyher Irid. 97*) pro parte, including also *G. exscapus.*

Plants 12–20 cm high. *Corm* globose, 12–16 mm diam., tunics brown, concentric, the layers fragmenting irregularly, the segments drawn into points above. *Cataphyll* pale, membranous, apparently solitary. *Leaves* 2–3, linear to ensiform, sticky on the sheath, margins and midrib and with sand adhering, the margins expanded at right angles to blade, midrib also enlarged and winged, blade thus broadly 2-grooved on each surface, the lowermost leaf basal, largest, usually exceeding the spike, to 28 cm long, the other leaves very short, becoming bract-like, and sheathing for half their length, the lower of these basal or sub-basal, the upper inserted in the mid part of the stem. *Stem* inclined, flexed above the sheath of the second leaf and at the base of the spike, occasionally with a short branch. *Spike* (2–)4–9-flowered, nearly horizontal, flexuose; *outer bracts* (14–)16–25 mm long, herbaceous, the inner membranous, about half as long. *Flower* zygomorphic, stamens and style declinate, the tepals white with pale pink veins, these sometimes coloring late, turning pink on fading; *perianth tube* 14–20(–25) mm long, shortly exserted from the bracts, curving near the apex; *tepals* 17–27 mm long, (5–)7–9 mm wide, the outer wider and shorter than the inner. *Filaments* unilateral and declinate, held above the lowermost tepal, 10–15 mm long; *anthers* unilateral, horizontal, 4–6 mm long. *Ovary* 3–4 mm long, *style* declinate, curving below the filaments, dividing near the apex of the anthers, branches 2–3 mm long, ultimately recurved. *Capsule* oblong to narrowly obovoid, 12–18 mm long. *Chromosome number,* $2n = 26$ (*Goldblatt 122, 6267*).

Flowering time. September to October.

Distribution. Stony soil on shale or sand, Olifants River Valley and the mountains from Pikeniers Kloof to Gifberg. Figure 52.

Geissorhiza longifolia has been known since at least the 1820s when specimens were collected by Ecklon and Zeyher in the Olifants River Valley (*Ecklon & Zeyher Irid. 97*). This collection, fairly widely distributed in herbaria, is usually mixed comprising also *G. confusa* and *G. exscapa* and it was to the latter (as *Acidanthera tubulosa*) that specimens were subsequently assigned. Ecklon gave specimens of this collection number the ms. name *Gladiolus costatus,* but this epithet was used in print (Ecklon, 1827) only for specimens from the Caledon district, now *G. schinzii.* Thus it was only when Lewis (1941) published her study of those species of *Acidanthera* that she assigned to *Engysiphon,* that *G. longifolia* was formally described.

The species has a fairly wide range, extending from Michells Pass northwards along the north–south trending western Cape mountains as far as the Gifberg. It grows most frequently in heavier soils, either in stony shale or in light clay, this in contrast to the other species of section *Engysiphon,* which grow in coarse quartzitic sand. *Geissorhiza longifolia* occurs both at lower altitudes, where clay soils are common, or in the mountains at low to middle elevations, but then most often in the shale band of the predominantly sandstone Table Mountain System.

Geissorhiza longifolia is distinctive in section *Engysiphon* in having comparatively small, white or pale pink flowers with a short perianth tube 14–20(–25) mm long and narrow tepals 17–27 mm long and 5–9 mm wide. It is sometimes confused with *G. confusa,* the two being similar in overall appearance. *Geissorhiza confusa,* however, has larger cream-colored flowers with a tube 25–40 mm long and tepals 28–40 mm long and 7–10 mm wide.

Specimens examined. SOUTH AFRICA. CAPE: 3118 (Vanrhynsdorp) slopes of Gifberg (DC), *Goldblatt 375* (BOL), *Phillips 7509* (NBG), *Compton 20776* (NBG), *Werdermann & Oberdieck 497* (B, K, PRE).

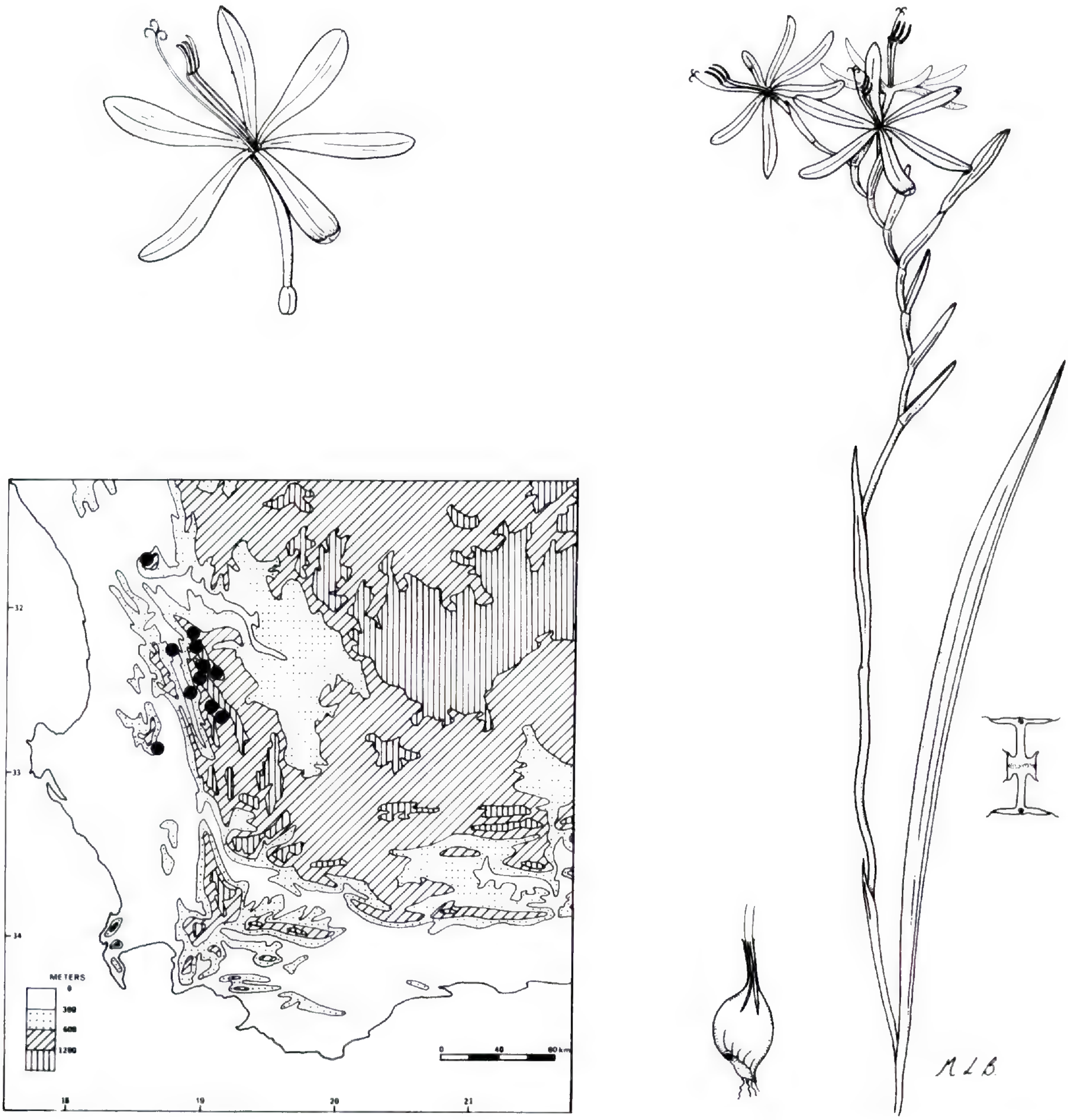


FIGURE 52. Morphology and distribution of *Geissorhiza longifolia*. Habit and corm ×0.5; flower life size; leaf section much enlarged (*Goldblatt 6267*, N of Citrusdal).

3218 (Clanwilliam) 10 mi. N of Clanwilliam (BB), *Compton 17116* (NBG, PRE); "Clanwilliam, am Fluss Olifantrivier," *Ecklon & Zeyher Irid. 97* (MO); Langevallei (BC), *Compton 5418* (BOL, NBG); Lambertshoek Berg (BC-BD), *Barker 6704* (NBG); summit of the ridge between Jakkals Valley and Kransvlei, sandy ground, 2,100 ft. (BD), *Oliver 3876* (STE); Kransvlei Berg, *Barker 4755* (NBG); old Clanwilliam road, S of the Algeria turnoff, *Goldblatt 287* (BOL); De Hoek, Piketberg (DC), *Lewis 1865* (NBG).

3219 (Wuppertal) E slopes of Pakhuis Pass (AA), *Goldblatt 6395* (MO); Pakhuis Pass in clay soil, *Leipoldt 794* (SAM), *Barker 4701* (NBG); Bosch Kloof, Cedarberg, *Pocock 248* (STE); Duiwelsgat, Cedarberg Mts. (AC), *Esterhuysen 13116* (BOL); Nieuwoudt Pass, 2,000 ft., *Leighton s.n.* (BOL 22558); Uitkyk Pass, *Barker 257* (NBG); Algeria, *Lewis s.n.* (BOL 22270); Kriedouw Krans Pass, between Alpha and Algeria, *Gillett 4121* (BOL, MO); Elands Kloof Pass (CA), *Barker 3102* (BOL, NBG); W end of Elands Kloof Pass, *Lewis 2515* (PRE, SAM 61822); Elands Kloof near Citrusdal, *Lewis 1340* (SAM), *Leighton 1252* (BOL); shale hillside N of Citrusdal, *Goldblatt 6267* (MO, PRE, S); Citrusdal rocks, *Barker 3766* (NBG); Elandskloof Bridge, 10 mi. SE of Citrusdal, *Maguire 1809* (NBG).

3319 (Worcester) flats below Michells Pass (AC), *Guthrie 3400* (NBG).

WITHOUT PRECISE LOCALITY: banks of the Olifants

River, 400 ft., *Schlechter 5030* (BOL, Z); sandveld between Greys Pass and Graafwater, *Leipoldt 3604* (BOL); Mostert Berg, *MacOwan 2506* (SAM); Clanwilliam, *Ecklon s.n.* (K); Olifants River Valley, *Ecklon & Zeyher s.n.* (76) (BM, PRE, Z).

44. Geissorhiza confusa Goldbl., sp. nov. TYPE: South Africa. Cape: Bains Kloof, *Schlechter 9162* (holotype, MO; isotypes, G, K). FIGURE 53.

Engysiphon exscapus (Thunb.) Lewis sensu Lewis, J. S. African Bot. 7: 23–24. 1941, pro parte excl. basion.

Sphaerospora exscapa (Thunb.) Klatt, Linnaea 32: 725. 1863, pro parte nom. illeg. gen. illeg. hom. (name applied to several allied species by Klatt).

Acidanthera tubulosa Baker, J. Linn. Soc., Bot. 16: 160. 1876, Handb. Irid. 186. 1892, Fl. Cap. 6: 132. 1896, pro parte (applied also to *G. exscapa*). The identity of the type specimen of this species is uncertain and the name is here rejected.

Freesia costata Ecklon ms., pro parte (also including *G. longifolia*).

Macrospathe secunda Pappe ms.

Planta 12–30 cm alta, foliis 2–3, inferiore basali ensiforme 4-sulcatoque, superioribus caulem vaginantibus, caule plerumque erecto, bracteis (30–)40–60 mm longis, spica florum 1–4(–8), floribus zygomorphis declinatis cremeo-flavis, tubo 25–40(–50) mm longo, tepalis 28–40 mm longis, antheris 6–8 mm longis, capsulo 15–23(–28) mm longo.

Plants 12–30 cm high. *Corm* globose, 12–18 mm diam., tunics brown, concentric, layers fragmenting irregularly, the sections drawn into long points above. *Cataphyll* pale, membranous, apparently solitary. *Leaves* 2–3, linear to ensiform or sometimes falcate, 3–7 mm wide, sticky on the sheath, margins, and midrib and with sand adhering, the margins and midrib heavily thickened, blade thus broadly 2-grooved on each surface, the lowermost leaf basal, largest, usually shortly exceeding the spike, to 30 cm long, the other leaves very short, becoming bract-like and sheathing for at least half their length, lower of these basal or sub-basal, the upper inserted in the mid part of the stem. *Stem* more or less erect, flexed at the base of the spike, rarely with a short branch. *Spike* inclined, 1–4(–8)-flowered, flexuose; *outer bracts* (30–)40–50(–60) mm long, herbaceous, the inner membranous, about half as long. *Flower* zygomorphic, the stamens and style declinate, cream to ivory with pale pink veins, turning pink on fading; *perianth tube* 25–40(–50) mm long, reaching to the apex of, or exserted to 15 mm from the bracts, curving near the apex; *tepals* 28–40 mm long, 7–10 mm wide, the outer wider and shorter than the inner. *Filaments* unilateral and declinate, held above the lowermost tepal; *anthers* unilateral, horizontal, 6–8 mm long. *Ovary* 5–8 mm long, *style* declinate, curving under the filaments, dividing near the apex of the anthers, branches 3–4 mm long, ultimately recurved. *Capsule* oblong to linear, 15–23(–28) mm long. *Chromosome number*, $2n = 26$ (*Goldblatt 483*).

Flowering time. October to December (to mid-January).

Distribution. Stony mountain soil in low fynbos, extending from French Hoek Pass to Gifberg. Figure 53.

Geissorhiza confusa has long been confused with other species of section *Engysiphon*. Baker (1892, 1896) placed specimens of this species in *Acidanthera tubulosa*, based on Houttuyn's interpretation of *Ixia tubulosa* Burman f., but excluding Burman's *Ixia tubulosa* itself, which he treated as a species of *Babiana*. I am treating *A. tubulosa* here as a nomenclaturally new species dating from 1878 when Baker proposed the combination *A. tubulosa* (Houtt.) Baker. It is thus typified by the figure published by Houttuyn, a good representation of a specimen in the Burman Herbarium in Geneva. This plant has long bracts, 45–54 mm long, flowers with a tube reaching only to the apex of the bracts, tepals to 22 mm long and anthers 5 mm long. The leaf is incomplete but appears to be of the kind with winged margins and poorly developed midrib. While the identity of this plant is questionable, it clearly is not the species here named *G. confusa*, which has shorter bracts, a larger flower, and broad leaves with a well-developed midrib. It matches both *G. exscapa* and *G. tenella* fairly well, and it is discussed in more detail under these species.

In 1941, Lewis used the name *Engysiphon exscapus* for *Geissorhiza confusa* believing that it was conspecific with Thunberg's *Gladiolus exscapus*, even though she had not then seen the type material of this species. As explained in detail under *Geissorhiza exscapa*, Thunberg's species is the plant Lewis named *E. longitubus*. The name must now therefore be applied to this species. This leaves a widespread and relatively well known plant without a name, and I propose for it the epithet '*confusa*,' which seems appropriate in view of the series of misunderstandings surrounding the name of this species.

Geissorhiza confusa is common in the western Cape mountains and extends from French Hoek Pass northwards through the Cold Bokkeveld and

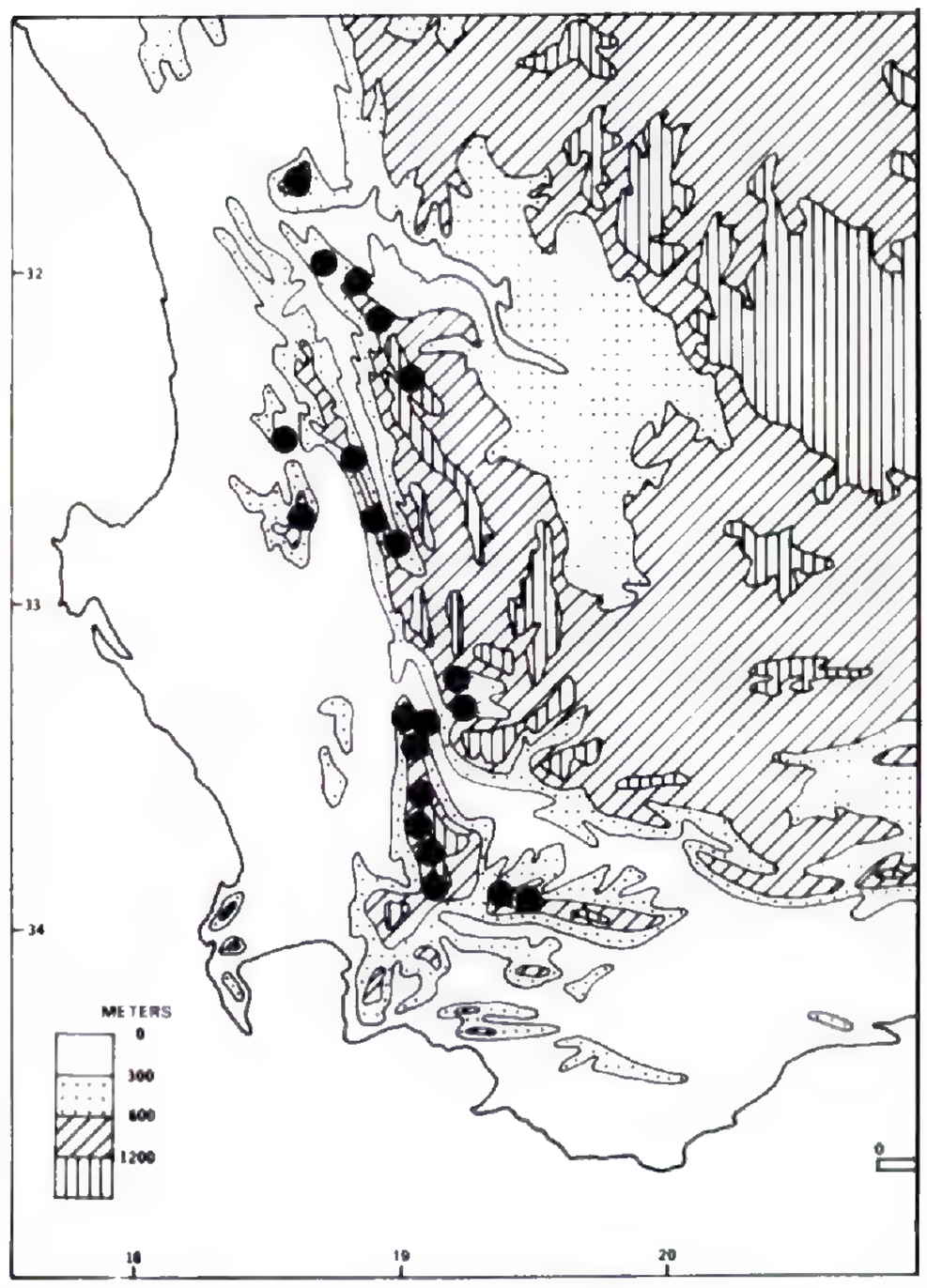


FIGURE 53. Morphology and distribution of *Geissorhiza confusa*. Habit ×0.5; flower life size; leaf section much enlarged (*Goldblatt 6836*, Bains Kloof).

Cedarberg Mountains to the Gifberg, also occurring on the outlying Piketberg Mountains. It grows on open stony slopes and flowers late in the year, sometimes into January. Its deep cream to almost yellow flowers are attractive and conspicuous when in bloom.

Several specimens that Lewis identified as *Geissorhiza confusa* (under the name *Engysiphon exscapus*), notably those from the Nieuwoudtville escarpment, have here been assigned to *G. exscapa*. These plants have a relatively long perianth tube not exserted from the bracts, often a feature of *G. confusa*, but all these specimens have the narrow, nearly terete leaf with margins raised into wings and poorly developed midrib characteristic of *G. exscapa*, while *G. confusa* invariably has a broader leaf with heavily thickened margins and midribs.

Geissorhiza confusa can occasionally be confused with the white- to pink-flowered *G. longifolia*, a short-tubed species with similar leaf morphology, but usually a several flowered spike of smaller, shorter tubed flowers [tube 14–20 (–25) mm long]. Specimens from the Het Kruis area, north of the Piketberg, notably *Bond 558* and *Compton 15529* bear up to ten flowers, may be branched, and have smaller bracts than other collections of the species. These may represent hybrids with *G. longifolia*, but this species has not been recorded in the area.

Geissorhiza confusa may also sometimes be difficult to distinguish from *G. schinzii*, especially when dry. *Geissorhiza schinzii* is restricted to the Caledon district, where it grows in habitats similar to *G. confusa*. It has pink flowers with tepals 9–15 mm wide, much broader than those of *G. confusa* and a perianth tube 24–32 mm long that seldom extends beyond the bracts. In contrast, *G. confusa* has narrow tepals, 7–10 mm wide, and a tube 25–50 mm long that may be exserted for as much as 10 or 15 mm from the bracts.

Specimens examined. SOUTH AFRICA. CAPE: 3118 (Vanrhynsdorp) Nardouw Mts., near Clanwilliam, sandy plateau (AC), *Bayliss 6107* (K, MO); Gifberg (AD), *Barker 9573* (NBG, STE), *Goldblatt 355* (BOL).

3218 (Clanwilliam) near Het Kruis (DA), *Bond 558* (NBG), *Compton 15529* (NBG), *Leighton 83* (BOL); top of Greys Pass (DB), *Hall 4186* (NBG); N side of the top of Versvelds Pass, Piketberg (DC), *Pillans 7148* (BOL, K); Piketberg Mt., *Maguire 1162* (BOL, NBG).

3219 (Wuppertal) Pakhuis Pass, near river camp (AA), *Barker 10315* (NBG); De Hangen, cave on the N slopes of Nardouwsberg, *Esterhuysen 32499A* (BOL); Wuppertal, *Thode A2086* (K); Klein Valley, Cedarberg (CA), *Taylor 1839* (NBG, STE); Cardouw Pass (CC), *Barker 7602* (NBG); Grootfontein, Olifants River Valley, SE of Grasruggens, 1,400 ft., *Oliver 3969* (STE).

3319 (Worcester) foot of the mt. above Porterville (AA), *Loubser 852* (NBG); mts. near Saron, *Schlechter s.n.* (S); Kluitjieskraal Forest Reserve, Zevenfontein, 1,600 ft., *Haynes 243* (STE); Waterfall Forest Reserve, NE slopes of Ontongskop, 1,400 ft. (AC), *Haynes 236* (STE); Tulbagh Mts. near Waterfall, *Herre s.n.* (STE 8973); Tulbagh Waterfall, *Compton 12412* (NBG), *H. Bolus 5253* (BOL, K); Castle Rocks, Ceres (AD), *Esterhuysen 14705* (BOL, PRE); rocky slopes, Michells Pass, *Lewis 5680* (NBG); Klein Berg, Hex River Mts., sandy plateau, *Esterhuysen 9534* (BOL, K); Bains Kloof (CA), *Salter 5118* (BM, BOL, K), *Barker 636* (NBG), *Lewis 855* (SAM 56196, K), *Thorne s.n.* (SAM 46473), *Compton 16813* (NBG), *Goldblatt 483* (BOL), *Schlechter 9162* (BM, G, K, MO, PRE); slopes N of Bains Kloof, *Goldblatt 6836* (MO, PRE); Baviaans Kloof, *Lewis 980* (SAM); Haalsneeuwkop, *Stokoe s.n.* (SAM 56191); Wemmershoek Valley, in stony sand (CC), *Esterhuysen 17677* (BOL, NBG, PRE); Du Toits Kloof, *Drège s.n.* (*Gladiolus flexuosus* Ker α) (G, K, MO), *Jackson s.n.* (NBG 121302); Zachariashoek, Kasteelkloof catchment, *Smith 67* (STE), *Haynes 261* (STE); top of French Hoek Pass, *Salter 4180* (BM, BOL, K); Drakenstein Mts., near French Hoek Pass, *Galpin 12284* (K, PRE); E side of French Hoek Pass, *Compton 8184* (NBG); Silver Streams, in Waterkloof, E of Villiersdorp (CD), *Oliver 5486* (PRE, STE); Jonas Kop, at the second gate (DC), *Strauss 74* (NBG);

WITHOUT PRECISE LOCALITY: Witsenberg and Skurfdeberg, Tulbagh, *Zeyher 1607A* (K, G); Caledon District, *Pappe s.n.* (*Macrospathe secunda* Pappe ms.) (K).

45. Geissorhiza bonae-spei Goldbl., sp. nov. TYPE: South Africa. Cape: between Fish Hoek and Sun Valley, on N-facing slopes after fire, *Goldblatt 5917* (holotype, MO; isotypes, K, PRE, S). FIGURE 54.

Engysiphon pictus (Foster) Lewis sensu Lewis, J. S. African Bot. 7: 21. 1941, Fl. Cape Penins. 252. 1950, pro parte excl. basion. (= *G. exscapa*).

Planta 12–20 cm alta, foliis 3 vel 2, inferiore longissimo basali tereto, marginibus alatis circum costis incurvatis, superiore caulem vaginante, caule erecto, spica florum 1–5, bracteis 2.5–3.7 cm longis, floribus zygomorphis declinatis carneis, tubo 20–30 mm longo, tepalis 24–27 mm longis, antheris 4–5 mm longis, capsulo 15–20 mm longo.

Plants 12–20 cm high. *Corm* globose, ca. 8 mm diam., asymmetric, with one side somewhat flattened below, tunics brown, concentric, fragmenting irregularly, segments drawn into short cusps above. *Cataphyll* membranous, evidently solitary, sometimes apparently lacking. *Leaves* usually 3, or 2, more or less terete, sticky on the sheath and blade and often covered with sand, the margins expanded into wings held at right angles to blade and curving inwards, thus making the leaf appear terete with 2 narrow longitudinal grooves, the lowermost leaf longest, basal, usually reaching to the apex of the spike, the second much shorter, also basal and often sticky, sheathing lower half of stem, free above, the uppermost leaf inserted in the mid part of the stem and sheathing for half to two-thirds its length, sometimes reduced and bract-like. *Stem* erect, simple, flexed above the sheathing parts of the leaves. *Spike* 1–5-flowered, flexuose; *outer bracts* green, 2.5–3.7 cm long, often dry towards apices, the inner membranous, much shorter than the outer. *Flower* zygomorphic with the stamens and style declinate, the tepals pale pink, deeper pink on the reverse and on the veins; *perianth tube* 20–30 mm long, slender, reaching the apex of the bracts or shortly exserted, curved near the throat; *tepals* oblong, obtuse, sometimes acuminate, 24–27 mm long, 5–7 mm wide, the inner somewhat narrower and longer than the outer. *Filaments* 14–16 mm long, unilateral and declinate, held above the lowermost tepal; *anthers* horizontal, more or less unilateral, 4–5 mm long. *Ovary* 4–5 mm long, *style* declinate, lying under the filaments, dividing near the mid part of the anthers, branches 2–3 mm long, recurved. *Capsule* oblong, 15–20 mm long, enclosed in the bracts. *Chromosome number*, $2n = 26$ (*Goldblatt 5267*).

Flowering time. Late September to mid-November.

Distribution. Stony, sandstone soils on slopes and flats in the southern Cape Peninsula; blooming mainly after fires. Figure 54.

Geissorhiza bonae-spei is closely allied to *G. tenella* and the two are sometimes difficult to distinguish when dry. *Geissorhiza bonae-spei* has large pink flowers that have tepals 24–27 mm long and 5–7 mm wide, and a tube 20–30 mm long, while the white-flowered *G. tenella* has shorter tepals 14–22 mm long and 3–4.5 mm wide, and a tube usually 30–40 mm long. The perianth tube and bracts of *G. tenella* are typi-

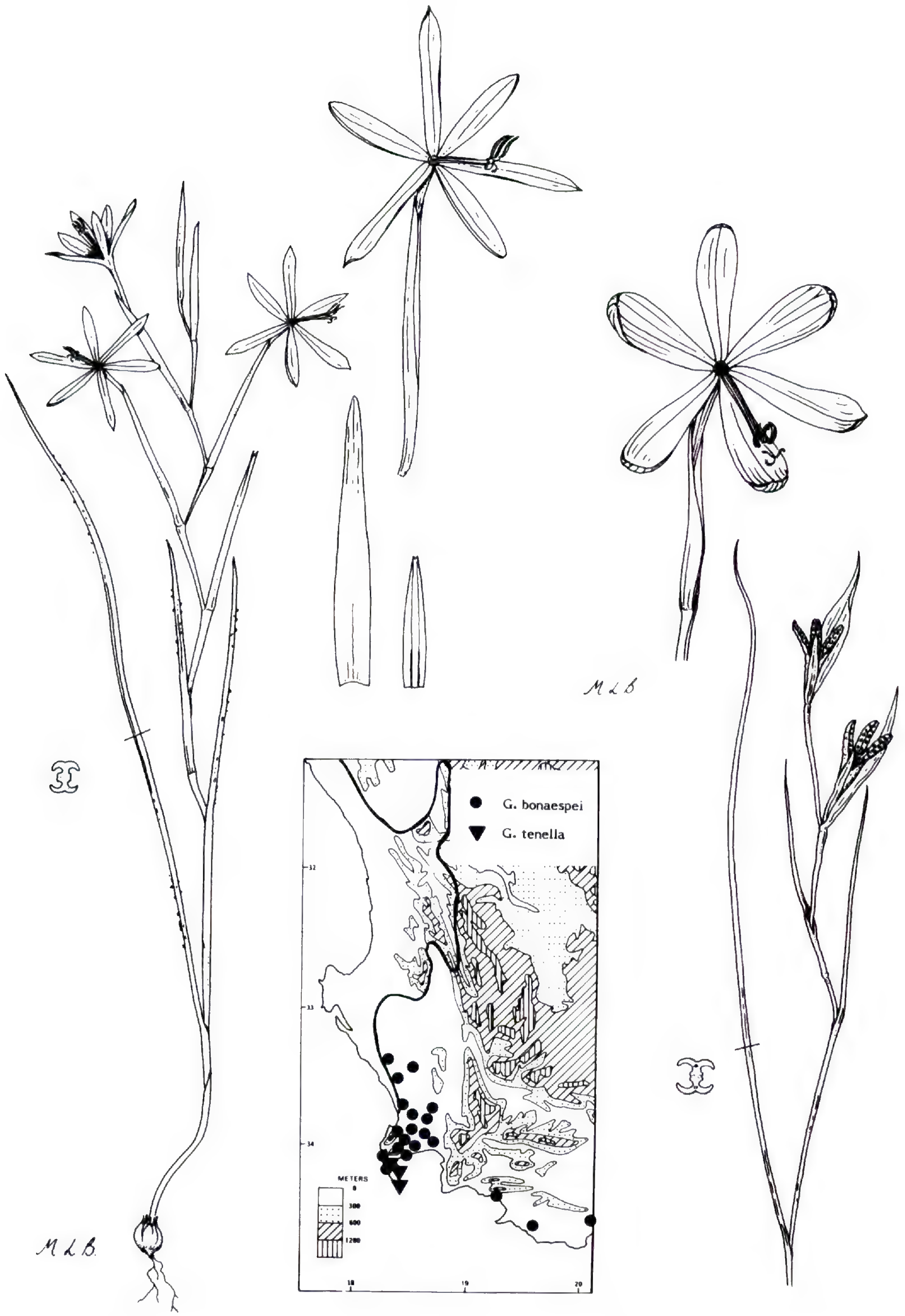


FIGURE 54. Morphology and distribution of *Geissorhiza tenella* (left) and *G. bonae-spei* (right) with the main range of *G. exscapa* outlined. Habits ×0.5; flowers and separated bracts life size; leaf sections much enlarged (*G. tenella, Goldblatt 7111,* near Koeberg; *G. bonae-spei,* fruiting *Goldblatt 5267,* foot of Klaasjagersberg, flowering *Goldblatt 5276,* Fish Hoek Mts.).

cally longer than those of *G. bonae-spei* in spite of the larger tepals of the latter.

Lewis used the name *Engysiphon pictus* for this species, but this name is a nomen novum provided by Foster (1936) for the plant figured by Houttuyn (1780) as *Ixia tubulosa* Burm. f., the type of which is a species of *Babiana,* now *B. tubulosa* (Lewis, 1959). The identity of Houttuyn's plant, a drawing of a specimen in the Burman Herbarium in Geneva, is somewhat problematic, but it is probably *G. exscapus.* The specimen is incomplete, but what remains of the leaf indicates a more robust blade than that found in any collection of *G. bonae-spei* known. In addition, the floral bracts are 4.5–5.5 mm long, substantially longer than in any collection of *G. bonae-spei* that I have seen. It therefore seems almost certain that the name *E. pictus* must be applied to another species. *Geissorhiza bonae-spei* is evidently endemic to the southern Cape Peninsula where it occurs on stony flats and slopes. It blooms well only after a fire the previous summer, and although quite common throughout its range, it is not often seen. Despite its growing relatively near to Cape Town, it was apparently first collected only early this century, by H. Bolus. The locality for this collection, given as the Riversdale district, must be regarded, in the light of current knowledge, as incorrect.

Specimens examined. SOUTH AFRICA. CAPE: 3418 (Simonstown) Muizenberg Plateau (AB), *Kensit s.n.* (BOL 22564); Pecks Valley, Muizenberg, *H. Bolus s.n.* (BOL); Diep River flats, *Marloth 7154* (PRE); Clovelly, Cape Peninsula, *Walgate 409* (NBG); Fish Hoek Mt., *Barker 3248* (NBG), *Lewis 803* (SAM); near Fish Hoek, *Werdermann & Oberdieck 792* (K); between Fish Hoek and Sun Valley, on N-facing slopes after fire, *Goldblatt 5917* (K, MO, PRE, S); near Simonstown, *H. Bolus 4691* (BOL); hills W of Simonstown, *Fair sub Wolley Dod 2036* (BM, K); Klawer Valley, *Lewis 627* (SAM), *Salter 7825* (SAM), *Compton 5268* (BOL); burned lower slopes of Klaasjagersberg, *Goldblatt 5267* (K, MO); Patrys Vlei (AD), *Compton 12321* (NBG); slopes of Pauls Berg, Cape Point, *Barker 4296* (BOL, NBG), *Lewis 1497* (BM, SAM 38337); near Cirkels Vlei, *Salter 2846* (BM, BOL, K); near Buffels Bay, *Esterhuysen 19258* (BOL).

DOUBTFUL LOCALITY: Riversdale district, *H. Bolus 22561* (BOL).

46. Geissorhiza tenella Goldbl., nom. nov. pro *Acidanthera rosea* Schinz, Bull. Herb. Boissier, Ser. 2, 2: 222. 1894; Baker, Fl. Cap. 6: 132. 1896. TYPE: South Africa. Cape: "Spitze des Teufelberges bei Capstadt," 3,300 ft. ("montis Diaboli" on the label), *Schlechter 75* (lectotype, G, here designated; isolectotypes, B, K). *Engysiphon roseus* (Schinz) Lewis, J. S. African Bot. 7: 21. 1941, Fl. Cape Penins. 252. 1950. FIGURE 54.

Acidanthera sabulosa Schltr., Bot. Jahrb. Syst. 27: 101. 1900. TYPE: South Africa. Cape: sand dunes near Eerste Rivier, *Schlechter 9025* (lectotype, B, here designated; isolectotypes, BM, G, K, MO).

Gladiolus tenellus Ecklon, Topogr. Verz. Pflanzensamml. Ecklon 41. 1827, nom. nud. et ms. (*Ecklon & Zeyher Irid. 290*).

Plants (10–)15–30 cm high. *Corm* globose, 7–10 mm diam., asymmetric, with one side somewhat flattened below and extending downwards shortly, tunics brown, concentric, fragmenting irregularly, segments drawn into short cusps above. *Cataphyll* membranous, apparently solitary. *Leaves* usually 3, nearly terete, sticky on the sheath and sometimes on the blade, the margins expanded into wings raised at right angles to the blade and curving inward, the leaf thus appearing terete with 2 narrow grooves running its entire length, the midrib not, or very little thickened, the lowermost leaf longest, basal, reaching to the base of the spike, the second leaf also basal, sheathing the lower third of the stem, free above, the uppermost leaf inserted on the upper third of the stem and sheathing for about two-thirds of its length, often bract-like. *Stem* erect, slender, simple. *Spike* (1–)2–5-flowered; *outer bracts* green, (2–)3–4(–5) cm long, the inner membranous, half as long as the outer. *Flower* zygomorphic with the stamens and style declinate, the tepals white to pale pink, flushed pink on the reverse; *perianth tube* (20–)30–40(–50) mm long, slender, either reaching only to the apex of the bracts or exserted to 15(–25) mm, curved near the apex; *tepals* oblong to linear, acute, 14–23 mm long, 3–4.5 mm wide. *Filaments* ca. 14 mm long, unilateral and declinate, held above the lowermost tepal; *anthers* horizontal, (2.5–)3.5–4.5 mm long. *Ovary* ca. 4 mm long, *style* declinate, lying under the filaments, branching near the apex of the anthers, branches ca. 3 mm long. *Capsule* oblong, 12–20 mm long, enclosed in the bracts. *Chromosome number,* $2n = 26$ (*Goldblatt 7111*).

Flowering time. October to November (to mid-December).

Distribution. Sandy, seasonally wet flats, from Darling in the north to the Bredasdorp district in the east. Figure 54.

On transfer to *Geissorhiza, Engysiphon rosea* requires a new name as the existence of *G. rosea* N. E. Br. (a synonym of *G. heterostyla*) prevents

the transfer of this epithet to the genus. The name *G. tenella* is here proposed for the species. A second synonym, *Acidanthera sabulosa* Schltr. likewise cannot be used in *Geissorhiza,* as the name *G. sabulosa* Klatt (a synonym of *G. imbricata* subsp. *imbricata*) blocks its transfer. The epithet 'tenella,' as *Gladiolus tenellus,* was used for the species by Ecklon (1827) and on labels for his collection of the species from the Cape flats, but no description was ever provided. It seems appropriate to validate this name for the species.

Geissorhiza tenella apparently has a relatively wide range, occurring on sandy flats and plateaus from the west coast near Darling, across the Cape Flats and Agulhas Peninsula to Cape Infanta. It is allied to the very long-tubed west coast species, *G. exscapa,* and to the southern Cape Peninsula species, *G. bonae-spei.* These three species all share a similar and distinctive leaf, in which the margins have well-developed wings that curve over the blade, while the midrib is not, or only very little thickened. This gives the leaf a terete appearance especially when dry (Fig. 54). *Geissorhiza bonae-spei* is readily distinguished by its 20–30 mm long perianth tube and pink, relatively broad tepals, some 24–27 mm long and 5–7 mm wide, in contrast to a (20–)30–50 mm long tube and white, very narrow tepals, some 14–23 mm long and 3–4.5 mm wide of *G. tenella.*

Flower size is unusually variable in *Geissorhiza tenella.* Plants from the east of its range, in the Caledon and Bredasdorp districts (as well as some from the Cape Flats), have a relatively short perianth tube, some 24–30 mm long and tepals 12–15 mm long (*Compton 22185, Goldblatt 675*). Most specimens collected on the Cape Flats and along the west coast often have much larger flowers in which the tube may be 40–50 mm long and the tepals to 23 mm long. Such specimens approach *G. exscapa* in their flower size and the relationship between these two species is discussed further under *G. exscapa.*

Specimens examined. SOUTH AFRICA. CAPE: 3318 (Cape Town) Darling Flower Reserve (AC), *Lewis 5744* (NBG); Riverlands, sandy wet flats (BC), *Esterhuysen 35084* (BOL, MO); Pella turnoff, Mamre road (CA), *Barker 10351* (NBG); E of Melkbosch Strand, *Salter 4889* (BM, K); between Melkbosch Strand and Mamre, *L. Bolus s.n.* (BOL 19976, K); Melkbosch road (CD), *Barker 1980* (NBG); summit of Devils Peak, *Schlechter 75* (B, G, K); Table Mt. above Oranjezicht, *Marloth 10714* (PRE); Camp Ground, *Wolley Dod 3419* (BOL, K); Claremont Flats, *Guthrie 1347* (BOL); burned slopes between Melkbos turnoff and Koeberg (DC), *Goldblatt 7111* (MO, STE, WAG); Kuilsrivier, *Pappe s.n.* (K, SAM 21118); Kuils River, *Worsdell s.n.* (K); Blackheath, flats SE of Leykor factory, *Oliver 4057* (K, PRE); Hercules Pillar (DD), *Barker 4855* (NBG); near Joostenberg, sandy flats, *Esterhuysen 16009* (BOL, NBG).

3418 (Simonstown) Chapmans Bay, Cape Peninsula (AB), *Lewis 473* (SAM); Muizenberg, *Pappe s.n.* (SAM 21121); Bergvleit farm, Ladies Mile, *Purcell s.n.* (SAM 90094); Cape Flats, near the German Church, Wynberg, *Kensit s.n.* (BOL 13419); Cape Flats, ¼ mi. SE of Retreat, *Pillans 8900* (BOL); Olifantsbosch, Cape Point (AD), *Lewis 1112* (SAM); Doornhoogte, Cape Flats (BA), *Ecklon & Zeyher Irid. 290* (78.11) (G, MO); sand dunes near Eerste Rivier, *Schlechter 9025* (B, BM, G, MO); flats near the Nuclear Institute, Faure, *Oliver 4059* (MO, STE); near Faure, *Boucher 3228* (PRE, STE).

3419 (Caledon) Kleinmond (AC), *Loubser 963* (NBG); Hermanus, W end of the town, *Goldblatt 675* (BOL); Die Mond, Voelklip, Hermanus, *S. Williams 527* (MO); Groot Hagelkraal, Haelkraal River area, NE of the farmstead (DA), *Oliver 6130* (PRE, STE).

3420 (Bredasdorp) De Hoop-Potberg Nature Reserve, Potberg farm (BC), *Burgers 1416* (STE); Bontebok Park, Bredasdorp (CA), *Compton 22185* (NBG).

47. Geissorhiza exscapa (Thunb.) Goldbl., comb. nov. *Gladiolus exscapus* Thunb., Prod. 2: 184. 1800, Skr. Naturhist.-Selsk. 6: 3, fig. 1. 1810. *Engysiphon exscapus* (Thunb.) Lewis, J. S. African Bot. 7: 23–24. 1941 (name applied to *G. confusus* Goldbl.). *Sphaerospora exscapa* (Thunb.) Klatt, Linnaea 32: 725. 1863, pro parte, nom. illeg. gen. illeg. hom. (name applied to several allied species). *Acidanthera exscapa* (Thunb.) Baker ex Bouche & Wittmack, Monatsschr. Vereines Beförd. Gartenbaues Königl. Preuss. Staaten 19: 15. 1876; Baker, J. Linn. Soc., Bot. 16: 160. 1878, in syn. of *A. tubulosa*; Foster, Contr. Gray Herb. 114: 44. 1936. TYPE: South Africa. Cape: origin unknown, *Thunberg s.n.* "*Gladiolus exscapus α*" (lectotype, Herb. Thunb. 1022 UPS, here designated); *Thunberg s.n.* "*Gladiolus exscapus β*" (syntype, Herb. Thunb. 1023 UPS). FIGURE 55.

Gladiolus thunbergii F. G. Dietrich, Nachtr. Vollst. Lex. Gärtn. 3: 494. 1817, nom. superfl. pro *G. exscapus* Thunb.

Acidanthera tubulosa Baker, J. Linn. Soc., Bot. 16: 160. 1878, Handb. Irid. 186. 1892, Fl. Cap. 6: 132. 1896, pro parte (applied also to *G. confusa*). *Acidanthera tubulosa* N. E. Brown, Kew Bull. 1929: 137. 1929, hom. illeg. *Acidanthera picta* Foster, Contr. Gray Herb. 114: 43–44. TYPE: South Africa. Cape: without precise locality, Herb. Burman (lectotype, G, here designated).

Ixia tubulosa Burm. f. sensu Houtt., Nat. Hist. part 2, 12: 36–37, tab. 78, fig. 2. 1780.

Engysiphon pictus (Foster) Lewis non sensu Lewis, J.

S. African Bot. 7: 21. 1941, Fl. Cape Penins. 252. 1950 (applied to *G. bonae-spei*).

Engysiphon longitubus Lewis, J. S. African Bot. 7: 24. 1941. TYPE: South Africa. Cape: Warm Baths, Clanwilliam, *Leipoldt s.n.* (holotype, BOL 20840).

Plants 18–32 cm high. *Corm* globose, 10–15 mm diam., tunics brown, concentric, layers fragmenting irregularly, segments drawn into short points above. *Cataphyll* pale, membranous, apparently solitary. *Leaves* 3, linear or appearing nearly terete, sticky on the sheath and blade, often with adhering sand, the margins expanded into wings held at right angles to the blade and curving inward, the blade thus appearing nearly terete with 2 longitudinal grooves, the midrib not or barely raised, the lowermost leaf basal, largest, reaching to about the base of the spike, the second similar but shorter, the third becoming bract-like and partly sheathing, inserted on the mid part of the stem. *Stem* sometimes very short, often sheathed almost entirely by the leaves, flexed above the sheath of the second leaf and inclined to horizontal, also flexed towards the base of the spike, usually unbranched. *Spike* inclined to horizontal, (1–)3–9-flowered, flexuose; *outer bracts* (30–)45–65 mm long, herbaceous, the inner membranous, much shorter, to 20 mm long. *Flower* zygomorphic, the stamens and style declinate, the tepals cream to ivory with darker veins, reddish on the reverse, turning reddish on fading; *perianth tube* 4–8 cm long, usually well-exserted from, or occasionally reaching only to the apex of the bracts, curving near the throat; *tepals* 26–35 mm long, 4.5–6 mm wide, the outer wider, and shorter than the inner. *Filaments* unilateral and declinate, held above the lowermost tepal; *anthers* unilateral, horizontal, 6–7 mm long. *Ovary* 6–9 mm long, *style* declinate, curving below the filaments, dividing near the apex of the anthers, branches ca. 3 mm long, ultimately recurved. *Capsule* oblong-elliptic, to 20 mm long. *Chromosome number*, $2n = 26$ (*Goldblatt 7061*).

Flowering time. September to October.

Distribution. Deep sandy soils along the west coast, from Blouberg near Cape Town in the south to near Hondeklipbaai in Namaqualand, also occasional in the mountains from Pakhuis Pass to the Nieuwoudtville Escarpment. Figure 55.

Although *Geissorhiza exscapa* was first described in 1800 (Thunberg, 1800), it has remained poorly understood. This was a result partly of the confusion of this species with several other taxa including *G. tenella, G. schinzii,* and *G. confusa,* and then when the systematics of the alliance was revised by Lewis (1941) and these species were treated as distinct, the type material was not critically examined. Thus in Lewis' revision of *Engysiphon,* to which she assigned all of these species, *G. exscapa* was described as a new species, *E. longitubus,* while the combination *E. exscapus* was applied to the species here named *G. confusa.*

The type material of *Geissorhiza exscapa* consists of two sheets in the Thunberg Herbarium at Uppsala, which bear the annotations *Gladiolus exscapus* α (1022) and β (1023). The first sheet consists of five specimens of a species with a long perianth tube, 65–78 mm long, well-exserted from the long bracts, a very short, mostly underground stem and narrow, nearly terete leaves with winged margins and weakly developed midrib. The second sheet consists of fragments of a grass species and one *Geissorhiza* specimen, with similar long-tubed flowers, a robust leaf with raised and winged margins and poorly developed midrib and a well-developed above ground stem. The description and the specific epithet match closely the specimens on the first sheet, these in turn matching *Engysiphon longitubus* Lewis. The correct name for this species, now referred to *Geissorhiza,* must be *G. exscapa.* The species to which Lewis gave the name, having no synonym, is here described as a new species, *G. confusa.*

When first described, Thunberg's two line diagnosis mentioned only the ensiform and unribbed (enervosus) leaves and filiform tepal tube exceeding the spathes. The description, amplified later (Thunberg, 1810, 1818), and accompanied by an illustration, leaves no doubt about the identity of the species. While the description clearly applies to all the specimens on the first sheet, they may comprise more than one gathering, and accordingly a single specimen has been designated the lectotype.

The identity of *Acidanthera tubulosa,* a species at least in part, treated as synonymous with *G. exscapa* by Baker (1892, 1896) is in some doubt. *Acidanthera tubulosa* was based on the specimen that Houttuyn (1780) identified and figured as *Ixia tubulosa* Burm. f. Burman's *Ixia tubulosa,* was apparently based on four specimens, comprising three species (Brown, 1929). The description matches best the species of *Babiana,* of which there are two sheets, and *I. tubulosa* is today regarded as the basionym of *Babiana tubulosa* (Burm. f.) Ker (Lewis, 1959), and can be regarded

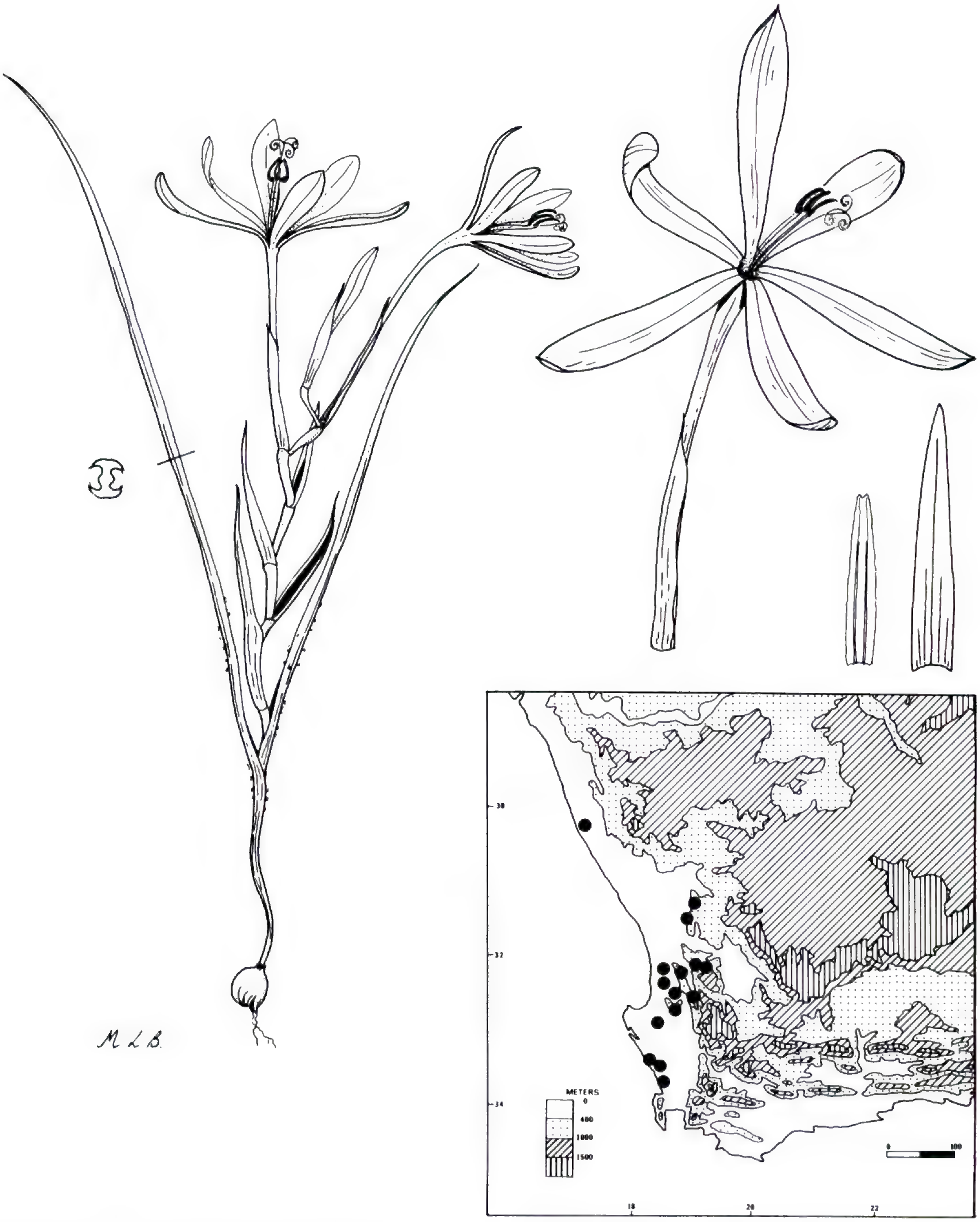


FIGURE 55. Morphology and distribution of *Geissorhiza exscapa*. Habit ×0.5; flower and separated bracts life size (*Goldblatt 7061*, top of Vanrhyns Pass).

as having been effectively lectotypified by Brown (1929). Baker was aware that the Burman species was identified with *Babiana* and he cited it in the synonymy of *B. tubiflora* in the "Flora Capensis." Thus his apparent combination *Acidanthera tubulosa* (Houtt.) Baker clearly excludes the type of Burman's *Ixia tubulosa* and *A. tubulosa* should be regarded rather as a new species dating from the time that the epithet was first used in *Acidanthera*. It is typified by the

figure published by Houttuyn and by the specimen on which the figure was based. The specimen in the Burman Herbarium is here designated as the lectotype.

This specimen has long bracts, 45–54 mm long, flowers with a tube reaching only to the apex of the bracts, tepals to 22 mm long, anthers 5–6 mm long and an incomplete leaf, clearly of the type with winged margins and poorly developed midrib. The identity of this plant is in doubt, as it does not match a specimen of any species exactly. However, it seems closest to *G. exscapa* and is here treated as a synonym of this species. The bracts and the perianth tube fall within the range recorded for this species (bracts normally 45–65 mm long, tube 40–80 mm long, typically but not always exserted) but the tepals, no longer than 22 mm are shorter than any recorded for *G. exscapa* in which they normally range from 26–35 mm long. The only other species that comes close to matching the specimen is *G. tenella* but this species has bracts and a tube only 20–40(–50) mm long, tepals 14–23 mm long, anthers 3–4.5 mm long, and a much narrower leaf than the one on the type specimen. Lewis identified *Acidanthera tubulosa* with *G. bonaespei* (as *Engysiphon pictus*), largely on the basis of the perianth tube not being exserted from the bracts. The bracts and the tube of *A. tubulosa* are, however, far too long for *G. bonae-spei,* while the flowers are much too small.

Despite the historic confusion between *Geissorhiza exscapa* and *G. confusa,* they do not seem particularly closely related. The distinctive leaf of *G. exscapa* with its broadly winged margins and poorly developed midrib, suggests that the species is closely allied to *G. bonae-spei* and especially to the slender and long-tubed *G. tenella* [*Engysiphon rosea* (Schinz) Lewis]. *Geissorhiza tenella* has a narrower leaf, shorter bracts and perianth tube, and there is not normally any confusion between the two species. However, specimens from the south of the range of *Geissorhiza exscapa,* notably *Esterhuysen 34420A* from Blouberg and *Compton 9817* from Mamre road, seem to intergrade with longer tubed specimens of *G. tenella.* The two species can, however, usually be distinguished by careful attention to size differences in the flowers. The largest flowered specimens of *G. tenella,* such as *Esterhuysen 35084* from Riverlands, *Wolley Dod 3419* from Camp Ground and *Esterhuysen 16009* from Joostenberg, have perianth tubes 35–40 mm long and tepals to 24 mm long and 4.5 mm wide. In contrast, the smallest flowered specimens of *G. exscapa* have a perianth tube at least 40 mm long and tepals 27 mm long by 5 mm wide.

Geissorhiza exscapa has its main range along the western Cape coast, where it extends from Blouberg, near Cape Town, to southern Namaqualand around Hondeklipbaai. It grows typically in deep alluvial coastal sands in sandveld vegetation with Cape taxa such as *Wiborgia* (Leguminosae) and *Wildenowia* (Restionaceae). It also occurs in similar habitats in the western Cape mountains between Pakhuis Pass and the Nieuwoudtville Escarpment where plants are generally taller and shorter tubed.

Several of the collections from the Nieuwoudtville Escarpment (*Strauss 60, Lewis 6114, 6119*) stand out in having the bracts rather shorter than usual, these being in the 3–3.5 mm range, in fact matching the bracts of *G. confusa.* The leaves in these collections are, however, quite typical of *G. exscapa* of which these plants seem merely to represent a short bracted form. Collections from the Pakhuis Pass area, *Compton 9627* and *Esterhuysen 3186,* as well as *Grant 3449* from Piketberg, also differ in having the perianth tube very shortly exserted from the bracts, and this gives the specimens an unusual appearance. Again, the leaves are typical and there seems no reason to revise the determination. In the absence of leaves, these plants can hardly be distinguished from *G. confusa,* in which the tube may occasionally be up to 50 mm long.

Specimens examined. SOUTH AFRICA. CAPE: 3017 (Hondeklipbaai) sand dunes between Wallekraal and Hondeklipbaai (AD), *Goldblatt 4226* (K, MO, NBG).

3118 (Vanrhynsdorp) top of Kobee Pass, ca. 15 mi. from Van Rhynsdorp (DA), *Strauss 60* (NBG); Nardouw Pass (DC), *Lewis s.n.* (BOL 22255).

3119 (Calvinia) Nieuwoudtville Escarpment between Meulsteenvlei and Clouds Kraal (AC), *Goldblatt 4332* (MO); top of Vanrhyns Pass at Meulsteenvlei, *Goldblatt 7061* (MO); Arendskraal farm near Nieuwoudtville, *Lewis 6119* (NBG); Meulsteenvlei, Calvinia, *Lewis 6114* (NBG), *Snijman 49* (NBG); 21 mi. S of Nieuwoudtville, Lokenburg (CA), *Story 4349* (K).

3218 (Clanwilliam) between Leipoldtville and Elands Bay (AB-AD), *Zinn s.n.* (SAM 59829); Graafwater (BA), *Zinn s.n.* (SAM 59828); 3.5 mi. NE of Graafwater, *Acocks 19764* (PRE); mts. above Clanwilliam (BB), *Bayliss 6109* (MO); Kranzvlei, Clanwilliam, *Leipoldt 4430* (BOL, NBG); 9 mi. N of Hopefield (CD), *Salter 3905* (BOL); near Het Kruis (DA), *Barnard s.n.* (SAM 68436), *Stephens 8612* (K); sandy flats NW of Eendekuil, *Howes 194* (PRE); near Piketberg (DC), *H. Bolus s.n.* (BOL 22563); Piketberg, *Grant 3449* (MO, PRE), *Marloth 6580* (PRE).

3291 (Wuppertal) Pakhuis (AA), *Esterhuysen 3186* (BOL); Pakhuis Pass, *Compton 9627* (NBG), *Emdon* 127 (STE); Warm Baths, Clanwilliam (CA), *Leipoldt s.n.* (BOL 20840).

3318 (Cape Town) near Hopefield (AB), *Garside 1631* (K), *Bachmann 855* (Z); Zonquasfontein ca. 8 km NW of the homestead, *Thompson 3512* (STE); Mamre road (CB), *Compton 9817* (NBG); Bokbaai, *van Rensburg 529* (PRE, STE), *557* (PRE); Blaauberg farm, inland from Blaauberg, in sandveld (CD), *Esterhuysen 3442A* (MO).

WITHOUT PRECISE LOCALITY: Cape of Good Hope (CBS), *Roxburgh s.n.* (BM).

SUBGENUS *GEISSORHIZA*

2. Subgenus Geissorhiza. TYPE: *G. obtusata* Ker.

Geissorhiza subgenus *Eugeissorhiza* Foster, Contr. Gray Herb. 135: 18. 1941, nom. illeg.

Corms with imbricate light to dark brown or blackish tunics, *leaves* lanceolate to ensiform or linear, blade plane, or with the margins and midrib and sometimes other veins thickened, or winged and ciliate-pubescent, *stem* smooth or ciliate-puberulous, *spike* few to several flowered, *bracts* herbaceous, often becoming dry above, ferrugineous in the upper half (sections *Ciliata* and *Planifolia*), *flowers* hypocrateriform, stellate or declinate, tube about as long as the bracts, or very short, stamens equal or unequal with one filament somewhat to much shorter than the other two.

Species. 34.
Distribution. Figure 18.

SECTION *INTERMEDIA*

8. Section Intermedia Goldbl., sect. nov. TYPE: *G. scillaris* A. Dietr.

Tunicae cormi plerumque pallide brunneae, foliis marginibus costique incrassatis, caule glabro, spica pluriflora, bracteis supra siccis, floribus stellatis, tubo brevi, staminibus aequalibus.

Corm tunics usually light brown, *leaves* with thickened margins and midribs, *stem* smooth, *spike* several flowered, *bracts* dry and membranous above, *flowers* stellate, tube short, stamens equal.

48. Geissorhiza similis Goldbl., sp. nov. TYPE: South Africa. Cape: W slopes of Redhill, near the top, *Lewis 2493* (holotype, SAM; isotypes, PRE, STE). FIGURE 56.

Planta 12–25(–35) cm alta, tunicis cormi imbricatis lignosis pallide brunneis, foliis 3, inferiore longissimo basali 1–2 mm lato, marginibus costisque incrassatis quadrisulcatisque, superiore infra caulem vaginante, caule erecto, raro ramoso, spica florum (2–)3–8, floribus stellatis, albis vel cremeis, tubo 2.5–3 mm longo, tepalis 9–12 mm longis, antheris ca. 3 mm longis, stylo diviso propre apicem antherarum, ramis recurvatis.

Plants 12–25(–35) cm high. *Corm* more or less symmetric, globose, 8–11 mm diam., tunics imbricate, woody, light brown, incised below into triangular, acute to truncate teeth. *Cataphyll* solitary, membranous, usually sticky and covered with sand. *Leaves* 3 (rarely 2), erect to falcate, linear, 1–2 mm wide, the margins and midrib enlarged and with 2 grooves running the length of each surface, edges of margin and midrib evidently smooth but often minutely ciliate to hispid, the lowermost leaf longest, basal, reaching to about the base of the spike, occasionally longer than the stem, the second much shorter, basal or inserted on the lower part of the stem, the uppermost leaf inserted on the mid part of the stem, usually short and sheathing below, occasionally reduced and entirely sheathing and bract-like, sheath ribbed, the lower two leaves often sticky below especially on margins, and with sand adhering even when dry. *Stem* erect, rarely branched, bearing a single small leaf or leafy bract in the mid part. *Spike* (2–)3–8-flowered, somewhat flexuose; *bracts* herbaceous, hyaline above and sometimes red-flushed, 4.5–7 mm long, the inner shorter than the outer. *Flower* stellate, white to cream, tepals spreading when fully open, the outer flushed pink on the reverse; *perianth tube* 2.5–3 mm long, shorter than the bracts; *tepals* 9–12 mm long, obovate, 5–6 mm wide. *Filaments* 2–3 mm long, equal; *anthers* 2–3 mm long, yellow. *Ovary* 1.5–2 mm long, *style* dividing at the apex of the anthers, branches to 2 mm long, recurved. *Capsule* unknown. *Chromosome number*, $2n = 26$ (*Goldblatt 7052, s.n.* no voucher, Bains Kloof).

Flowering time. Late August to October.

Distribution. From the southern Cape Peninsula and Hottentots Holland Mountains to Jonas Kop and Bains Kloof in the north, with an isolated record from the Cedarberg, in sandy mountain soil. Figure 56.

Geissorhiza similis resembles the apparently unrelated *G. hispidula* to such a degree in its leaves and flowers that if it had not been for the well-preserved corms of a few collections, notably *Thomas s.n.*, *Lewis 2493*, and *Barker 5911*, I would not have hesitated to regard specimens

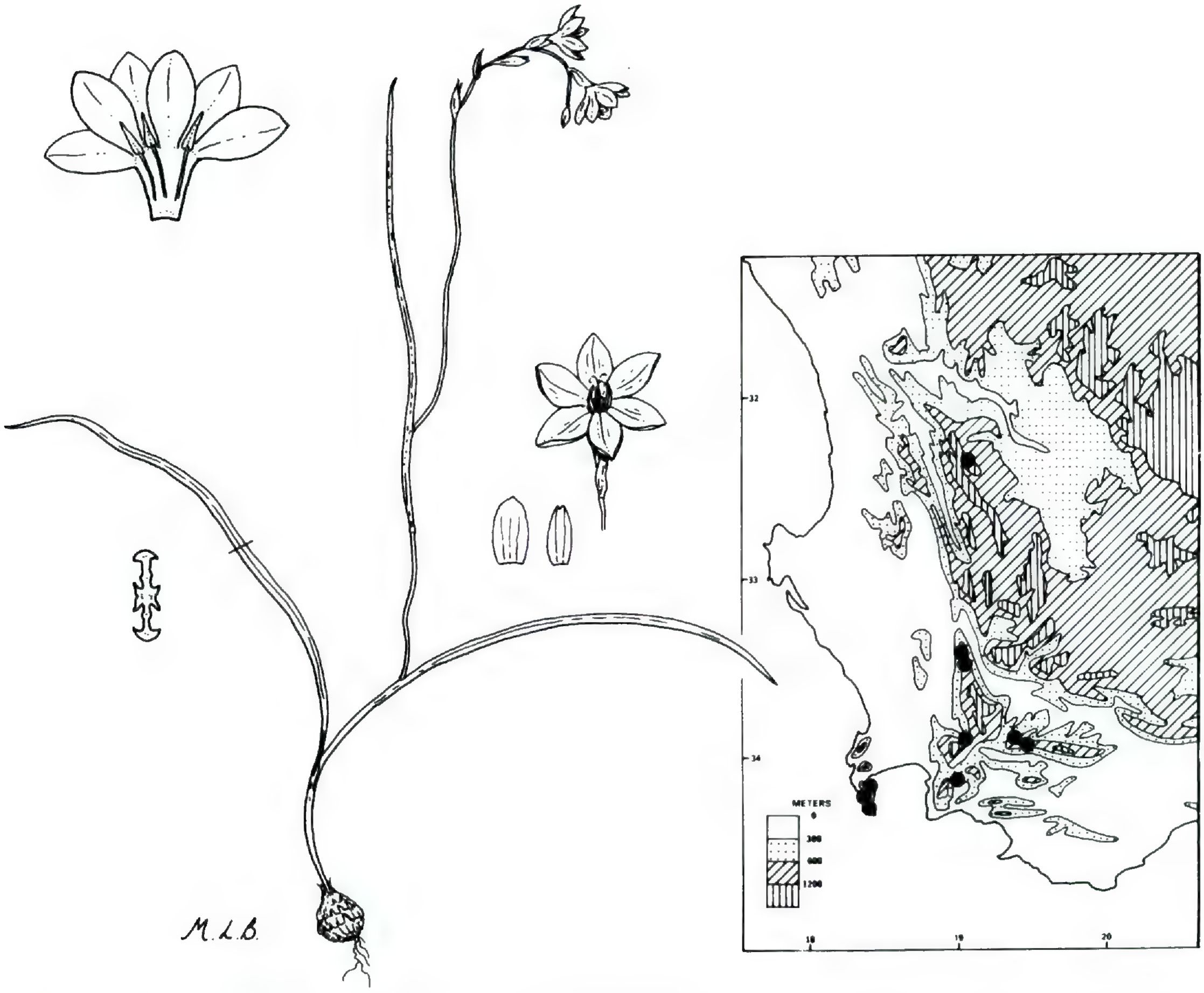


FIGURE 56. Morphology and distribution of *Geissorhiza similis*. Habit ×0.5; intact flower life size; partial flower and gynoecium ×2; leaf section much enlarged (*Goldblatt 7052*, mts. at Clovelly, Cape Peninsula).

of this species as no more than rather slender examples of *G. hispidula*. The corm tunics of *G. similis* are, however, clearly imbricate rather than concentric as in *G. hispidula*. This distinction is probably fundamental, and it suggests that these two species actually belong to different subgenera, imbricate corm tunics being a characteristic of subgenus *Geissorhiza*, while *G. hispidula* has concentric corm tunics typical of subgenus *Weihea*. The tunics of *G. similis* are unusual in subgenus *Geissorhiza* only being a light brown rather than blackish as in most species. In this respect they resemble those of *G. scillaris*, and it is to this species that it is most probably related. These two species have thus been placed in their own section, *Intermedia*.

A careful examination of *Geissorhiza similis* reveals several small ways in which it can be distinguished from *G. hispidula*. The leaves are softer in texture and only sticky below rather than throughout, and the bracts are not at all sticky so that they are free of adhering sand. The flowers of *G. hispidula* are a different color, being cream to pale yellow and usually have relatively dark reddish markings on the reverse of the outer tepals, while *G. similis* has white- to cream-colored flowers often not or only very lightly marked on the reverse of the outer tepals.

Taller and more slender specimens of *Geissorhiza similis* can easily be confused with *G. umbrosa* in the absence of corms. The two species are in fact very similar, although *G. umbrosa* has somewhat larger flowers and narrower leaves and it never has ciliate to hispid margins. When corms are available, *G. similis*, with its woody to stiffly membranous imbricate tunics, can always be distinguished from *G. umbrosa* which has soft membranous to fibrous and concentric corm tunics.

The recorded distribution of *Geissorhiza sim-*

ilis is the southern Cape Peninsula and the mountains across the Cape Flats from the Hottentots Holland Mountains to Jonas Kop in the Riviersonderend Mountains and Bains Kloof some 80 km to the north. There is also an isolated record from the Cedarberg. The species is relatively inconspicuous and easily overlooked and it seems likely that it occurs elsewhere in the southwestern Cape. Its range is likely to be extended with further collecting in the mountainous areas to the north and east.

Specimens examined. SOUTH AFRICA. CAPE: 3219 (Wuppertal) South Cedarberg, path from base of Sneeuberg to the Maltese Cross, in marshy area after fire (CA), *Esterhuysen 35669* (BOL, K, MO, PRE).

3319 (Worcester) Bains Kloof (CA), *Schelpe 4192* (BM, SAM), *Loubser 476* (NBG), *Strey s.n.* (M); Baviaans Kloof, off Bains Kloof, *Leighton 2158* (BOL, NBG); Upper Wellington Sneeukop, foot of cliffs, *Esterhuysen 21789* (BOL); French Hoek Pass, summit ridge of Middagkransberg (CC), *Boucher 2390* (K, PRE, STE); French Hoek Forest Reserve, *Leighton 281* (BOL); Jonaskop, 200–300 ft. below summit on E side (DC), *Esterhuysen 35630* (BOL, MO); Jonaskop, among rocks below summit on N side, *Goldblatt 6423* (K, MO, NBG, PRE, S).

3418 (Simonstown) Kalk Bay Mt. (AB), *Barker 4223* (NBG), *Goldblatt 3111* (MO); damp shaded SE-facing mt. slopes above Clovelly, *Goldblatt 7052* (K, MO, NBG, PRE, S, WAG); plateau between Kalk Bay and Steenberg Peak, *Lewis 4794* (PRE, SAM 57331); W slopes of Redhill, near top, *Lewis 2493* (PRE, SAM 61718, STE); between Redhill and Klaasjagers, *Lewis 2492* (SAM); Redhill, Simonstown, *Barker 5911* (NBG, STE), *Taylor 5244* (PRE, STE); Simons Bay, *Wright 248* (GH, K, L); Rooihoogte, Cape Peninsula, *Leighton 280* (BOL), *Compton 13788* (NBG); Glencairn Mt., *Compton 11583* (NBG); Cape Point Reserve (AD), *Thomas s.n.* (NBG 67496); Steenbras Mts., Rockview Dam site (BB), *Snijman 564* (MO, NBG).

3419 (Caledon) Boschmans Kloof, Elgin (AA), *Stokoe s.n.* (SAM 60197).

49. Geissorhiza scillaris A. Dietr., Sp. Pl. 6th edition, 2: 587. 1833; Goldblatt, Nordic J. Bot. 3: 441. 1983. *Ixia scillaris* Thunb., Diss. de *Ixia* no. 14: 146. 1783, hom. illeg. non L. (1762). *Ixia ramosa* Ker, Bot. Mag. 17: sub. tab. 549. 1802, nom. nov. pro *I. scillaris* Thunb. *Ixia phalangioides* Roem. & Schult., Syst. Veg. 1: 385. 1817, nom. superfl. pro *Ixia ramosa* Ker, but intended as a nom. nov. pro *I. scillaris* Thunb. TYPE: South Africa. Cape: without precise locality, *Thunberg s.n.* [lectotype, Herb. Thunb. 992 UPS, pro parte, designated by Goldblatt (1983); isolectotype, S], the type material at UPS comprises a mixture of *G. scillaris* and *G. juncea*; *Thunberg s.n.* [syntypes, Herb. Thunb. 992 UPS, pro parte, S = *G. juncea* (Link) A. Dietr., Herb. Thunb. 993 UPS = *G. imbricata* (de la Roche) Ker]. FIGURE 57.

Geissorhiza juncea var. *pallidiflora* (Schltr.) Foster sensu Foster, Contr. Gray Herb. 135: 23. 1941. As to most specimens cited but excl. type [= *G. juncea* (Link) A. Dietr.].

Plants slender, (12–)15–35 cm high. *Corm* globose, 8–12 cm diam., larger when old tunic layers numerous, tunics woody, rarely papyraceous, brown, imbricate, outer layers fragmenting regularly below into regular narrow truncate segments, drawn into bristles above. *Cataphyll* evidently solitary, often broken, sticky and with sand adhering. *Leaves* 2, sticky, often with adhering sand especially below, the lower leaf free from the base and erect to falcate, cruciform in section, with strongly raised margins and midrib and 4 broad grooves running the length of the leaf, the upper leaf sheathing almost entirely, enclosing the stem in the lower half or nearly to the base of the spike, the free apical part short, 1–3 cm long. *Stem* erect, flexed below the spike, with a greenish to white, membranous sheathing 7–12 mm long bract in the upper third, simple or rarely with a short branch in the axil of the stem bract. *Spike* 4–10(–20)-flowered; *bracts* green, becoming dry, transparent and pale or rarely brownish above, spreading in the upper part, 6–8 mm long, the inner shorter than the outer, 5–7 mm long. *Flower* stellate, white, bluish white or blue with a white center; *perianth tube* 1–1.5 mm long, infundibuliform; *tepals* ovoid, 8–9 mm long, 3–4 mm wide. *Filaments* 2–3 mm long, equal; *anthers* 2.5–3.5 mm, pollen creamy white. *Ovary* ca. 1.5 mm long, *style* 5–6 mm long, dividing at the apex of the anthers, the branches ca. 1 mm long, recurved. *Capsule* globose, 3–4 mm long, shorter than the bracts. *Chromosome number*, $2n = 26$ (*Goldblatt 5245*).

Flowering time. Mid-August to October (to December at high altitudes).

Distribution. Mountains of the western Cape from Elgin and Shaws Pass in the south to the northern Cedarberg, usually above 800 m. Figure 57.

Geissorhiza scillaris is to me a very distinct and isolated species, yet surprisingly since it was first collected by Thunberg in the 1770s has either been treated as conspecific with the superficially similar and well known *G. juncea* or regarded as an unnamed species. As pointed out by Lewis in unpublished notes with several Bolus Herbarium

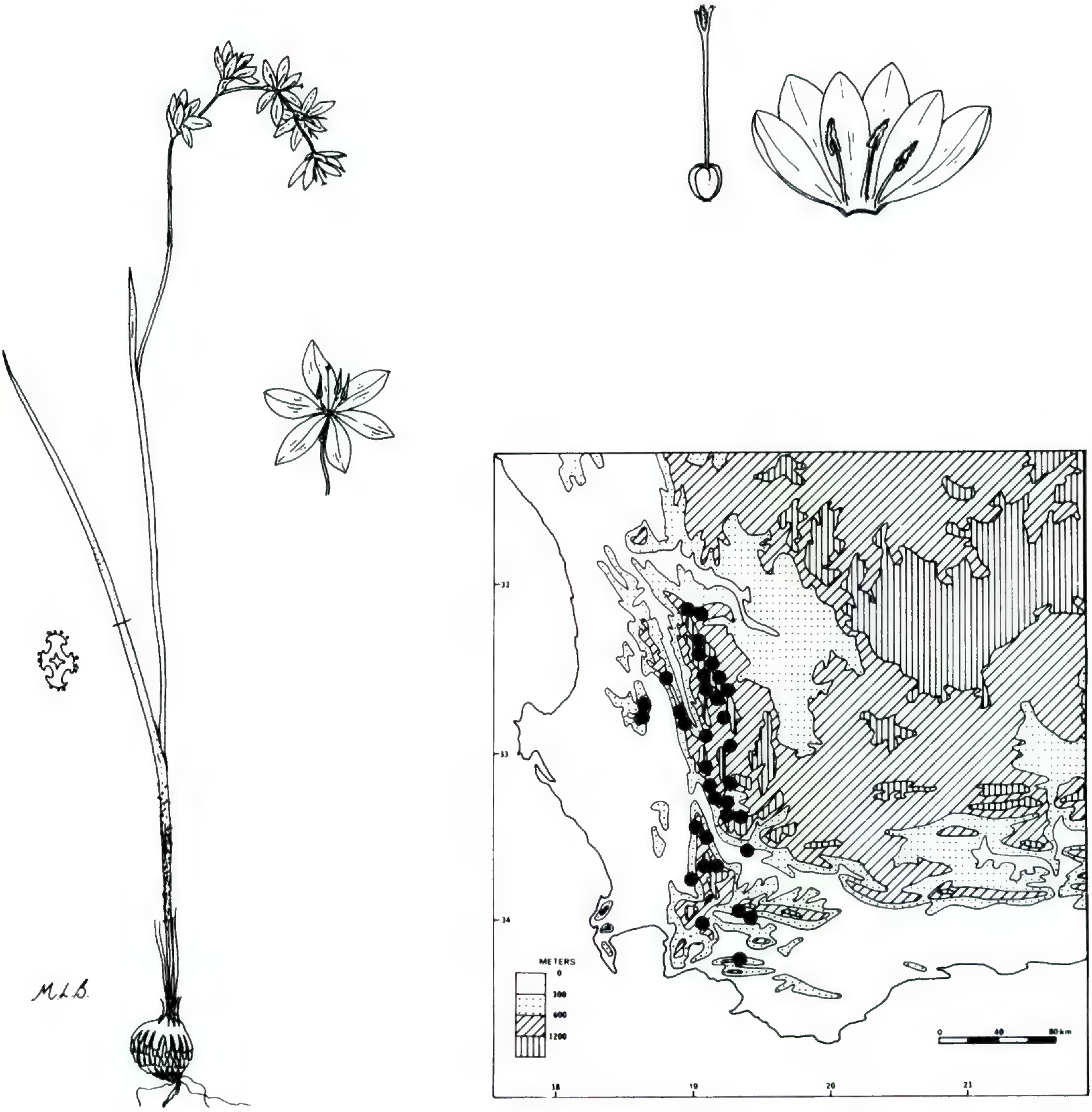


FIGURE 57. Morphology and distribution of *Geissorhiza scillaris*. Habit ×0.5; intact flower life size; partial flower and gynoecium ×2; leaf section much enlarged (*Esterhuysen 35495*, Zebrakop, Piketberg).

sheets, it differs from *G. juncea* in having only one free leaf instead of two, in having a second basal leaf sheathing most of the stem instead of a short third leaf only partly sheathing, and in having a different type of corm. Lewis could have added that *G. scillaris* is also distinctive in consistently having a short, membranous and sheathing bract on the upper part of the stem, a feature found rarely in *G. juncea*. The fact that *G. scillaris* was described, albeit from mixed material, as early as 1783 by Thunberg, as *Ixia scillaris* (an illegitimate homonym for *I. scillaris* L.) has largely been overlooked. Typification of Thunberg's illegitimate homonym, *I. scillaris*, is complex owing to the fact that the type material consists of three different taxa. The arguments leading to the selection of a lectotype have been dealt with in a separate paper (Goldblatt, 1983).

The subsequent history of *Ixia scillaris* is complex. The species was renamed *I. ramosa* by Ker (1802c) (who must have chosen the epithet from the protologue and not from the type material which he did not see). The name did not get taken into general use, and Ker (1827) later placed *I.*

ramosa in the synonymy of *Geissorhiza imbricata*. Roemer and Schultes (1817) also renamed *I. scillaris*, calling it *I. phalangioides*, but the epithet is illegitimate and superfluous for *I. ramosa* Ker, cited in synonymy. Schultes (1822) distinguished *I. scillaris* from *I. juncea* as did Dietrich (1833), who transferred *I. scillaris* to *Geissorhiza*, but few other authors have. Baker (1892, 1896), in his important treatments of Iridaceae, ignored the species, and Foster (1941) placed *I. scillaris* Thunb. in the synonymy of *G. juncea*. Foster and probably Baker did not see Thunberg's collections. Brown, who examined the Thunberg Herbarium, also failed to distinguish *G. juncea* from *G. scillaris*.

Foster actually recognized the species here called *Geissorhiza scillaris* as *G. juncea* var. *pallidiflora* (Schltr.) Foster without realizing that the type material of *G. scillaris*, at least in part, matched his variety. *Geissorhiza juncea* var. *pallidiflora*, based on *G. pallidiflora* Schltr., is typified by *Schlechter 9088*, a collection that appears to differ in no significant way from *G. juncea*. The type collection of *G. pallidiflora* is, however, interesting in one respect, in that of the many plants of the gathering, two at least have a membranous stem bract, but this is probably coincidence and not indicative of any relationship with *G. scillaris*.

It is difficult to place *G. scillaris* with certainty to subgenus, but the limited number of known corms have tunics of the imbricate type, though unlike the typical tunics of subgenus *Geissorhiza*, species of which have heavy black tunics. The brown corm tunics of subgenus *G. scillaris* tend to accumulate more than is usual in subgenus *Geissorhiza* and over the years become rather distorted and broken. The species is here assigned to the ditypic section *Intermedia* of subgenus *Geissorhiza*, together with *G. similis*, which has corms with similar tunics. The two species are otherwise rather different and although probably not closely allied, they appear to belong to a single, perhaps very old line.

Geissorhiza scillaris is a fairly common species in the mountains of the western Cape, and it extends north from Shaws Pass and the Groenland Mountains at Elgin to Pakhuis Pass in the northern Cedarberg. It usually grows in open rocky places, in sandstone-derived soil, and usually at altitudes above 800 m. It may occasionally be found in damp places, but is clearly well adapted to dry stony situations. Most populations consist of plants with white flowers, but in the Cold Bokkeveld and Cedarberg there is an attractive blue-flowered form in which the flower center is white (*Goldblatt 5072, Esterhuysen 3013, 20507, 13111*).

Specimens examined. SOUTH AFRICA. CAPE: 3218 (Clanwilliam) Mts. above The Rest, Pikeniers Kloof (DB), *Gillett 3740* (BOL); Zebrakop, Piketberg, *Esterhuysen 35495* (K, MO, NBG, PRE, S, WAG); Versveld Pass, Piketberg (DC), *Compton 10991* (NBG).

3219 (Wuppertal) Heuningvlei (AA), *Stokoe s.n.* (SAM 55682), *Esterhuysen 8061* (BOL); Koudeberg (Wuppertal), *Schlechter 8775* (B, BM, BOL, BR, E, G, H, K, L, MO, PH, PRE, Z); Cedarberg, Middelberg (AC), *Lewis s.n.* (SAM 52416), *Kerfoot 6115* (NBG), *Goldblatt 4133* (MO); Uitkyk Pass, Cedarberg, *Barker 267* (NBG); Elandskloof (CA), *Barker 3793* (NBG), *Lewis s.n.* (BOL), *Goldblatt 5245* (K, MO); Buffelshoek Pass, Middelberg, *Thompson 2948* (PRE, STE); Top of Buffelsberg Pass, Elandskloof road, *Goldblatt 2752* (MO, WAG); Middelberg, Elandskloof, *Hafstrom & Acocks 299* (PRE, S); Crystal Pool hut, *Pocock 674* (STE); Sneeuberg, summit, *Taylor 6152* (PRE, STE); road to Krom River farm (CB), *Goldblatt 5672* (K, MO, NBG, NSW, PRE, S, US, WAG); Kromme River, rocky ridge, *Esterhuysen 20507* (BOL, PRE); Krom River farm, sandy flats, *Goldblatt 5670* (MO); top of Dasklip Pass (CC), *Lewis 6217* (NBG); Waboomsrivier, Cold Bokkeveld, *Hanekom 631* (K, PRE); Cold Bokkeveld, near De Keur (CD), *Lewis 2504* (BOL, K); Porterville Mts., NW end of Zuurvlakte, *Thompson 1476* (STE).

3318 (Cape Town) Klein Drakenstein (DD), *DuPlessis s.n.* (STE).

3319 (Worcester) Visgat (AA), *Stokoe s.n.* (SAM 63132); Winterhoeksberg, *Ecklon & Zeyher Irid. 227* (72.11) (B, FI, G, MO); Great Winterhoek, *Marloth 2337* (PRE); Saron, Tulbagh, *Andrag s.n.* (STE 19780); Gydo Pass (AB), *Leighton s.n.* (BOL), *Compton 16229* (NBG); Gydouw, *Leipoldt 3812* (BOL); top of the Witsenberg, near Steendal (AC), *H. Bolus s.n.* (BOL 5744, K); slopes of the Witsenberg, *Phillips 1876* (SAM); Slab Peak, 4,000 ft., Michells Pass (AD), *Esterhuysen 6163* (BOL); Ceres, *Acocks 1809* (S), *Rogers 28733* (Z); Eselfontein, Ceres, *Esterhuysen 20362* (BOL, PRE); flats at head of Rooikloof, above Eselfontein, *Oliver 5089* (PRE, STE); flats NW of Prince Alfreds Hamlet, *Oliver 5016* (K, MO, PRE, STE); Mts. in Hex River Valley (?BC), *Tyson 722* (BOL, SAM); Wellington (CA), *Grant 2391* (BOL, BR, MO); Wolwehoek Forest Reserve, Bains Kloof, *Barker 4336* (NBG); Bains Kloof, *Compton 18266* (NBG); Mias Poort, above Du Toits Kloof, *Esterhuysen 35517* (BOL, MO, US, WAG); slopes at N end of Du Toits Kloof, *Esterhuysen 18912* (BOL, PRE); Molenaar's Peak, Du Toits Kloof, *Stokoe s.n.* (SAM 59845); Breede River flats near Worcester (CB); *Goldblatt 6980* (MO, PRE).

3419 (Caledon) Vijoens Pass (AA), *Werdemann & Oberdieck 395* (B, PRE); stony flats S of Villiersdorp at Theewater farms turnoff (AB), *Goldblatt 4014* (MO, PRE); hillside N of Theewater Kloof, above dam, *Goldblatt 4734* (MO); top of Shaws Pass, recently burned (AD), *Marsh 1432* (PRE, STE).

WITHOUT PRECISE LOCALITY: *Thungberg s.n.* ("*Ixia scillaris α*") (Herb. Thunb. 992 in part, S, UPS; Herb. Burman s.n., G).

SECTION *GEISSORHIZA*

9. Section Geissorhiza. TYPE: *G. obtusata* Ker.

Geissorhiza section *Rochea* Baker, J. Linn. Soc., Bot. 16: 93. 1878, nom. illeg. superfl.

Geissorhiza subsection *Ventricosae* Foster, Contr. Gray Herb. 135: 27. 1941. TYPE: *G. imbricata* (de la Roche) Ker, nom. illeg. superfl.

Corm tunics hard and woody, *stems* smooth, *leaves* with the margins and midrib and often other veins strongly thickened, ensiform to linear, or terete, *bracts* herbaceous below, becoming dry above, *flowers* stellate to hypocrateriform, actinomorphic or zygomorphic and declinate, the tube short or reaching to the apex of the bracts, stamens equal or unequal.

Species. 10.

50. Geissorhiza imbricata (de la Roche) Ker, Ann. Bot. (König & Sims) 1: 224. 1804; Baker, Handb. Irid. 156. 1892, Fl. Cap. 6: 72. 1896; Foster, Contr. Gray Herb. 135: 37. 1941, pro parte excl. var. *brehmii*; Lewis, Fl. Cape Penins. 255. 1950. *Ixia imbricata* de la Roche, Descr. Pl. Aliq. Nov. 17. 1766. TYPE: South Africa. Cape: Cape Peninsula, Lakeside, *Salter 7034* [neotype, BOL, designated by Goldblatt & Barnard (1970)]. FIGURE 58.

(For additional synonyms see under the subspecies).

Plants 6–25(–30) cm high. *Corm* 5–10 mm diam., globose, tunics blackish, imbricate, the outer layers accumulating above, and regularly notched below into segments. *Cataphyll* single, membranous, often lacking in dry material. *Leaves* 3, reaching from about middle to apex of spike, sometimes longer, ribbed with (2–)4 to several longitudinal grooves running the length of the leaf, the lower two basal, (linear to) ensiform, (1–)2–6(–10) mm wide, the third leaf largest, inserted on the stem near the base or in the lower part and sheathing below for half its length, the sheath strongly ribbed and inflated. *Stem* erect, simple or 1-branched, flexed above the leaf sheath. *Spike* (2–)6–8(–14)-flowered, flexed at the base and flexuose; *bracts* herbaceous below, often becoming dry and membranous above at flowering time, (6–)8–12(–15) mm long, sometimes red above, the inner narrower than the outer. *Flower* stellate to shallowly cupped, white to cream or pale yellow, usually red on the reverse of the outer tepals, sometimes dark in the center; *perianth tube* 2–8 mm long, enclosed to slightly exserted from the bracts; *tepals* (9–)11–25(–30) mm long, obovate, (4.5–)5.5–12 mm wide, obtuse. *Filaments* equal, (3–)4–8(–10) mm long. *anthers* (3–)4–7 mm long, yellow. *Ovary* 2–3.5 mm long, style dividing near the apex of the anthers, branches 3–4 mm long, recurved. *Capsule* oblong-globose, to 10 mm long. *Chromosome number*, $2n = 26$ (*Goldblatt 165*).

Flowering time. (August to) September to October.

Distribution. Southwestern Cape, from Bredasdorp north to the Olifants River Valley; mainly on damp poorly drained flats. Figure 58.

As treated here, *Geissorhiza imbricata* is one of the more variable species in the genus. It includes no less than three species recognized by Foster (1941) in his monograph of the genus: *G. wrightii*, *G. rubicunda*, and *G. bicolor* (including var. *macowanii*), as well as *G. sulphurea* var. *arenicola*.

The main forms or races of *Geissorhiza imbricata* are:

1. A short-tubed (2–4 mm) form, usually fairly low growing, with small, white to cream flowers that was once common on the Cape Peninsula and adjacent Cape Flats (*G. sabulosa*, *G. imbricata* sensu Baker and sensu Lewis).

2. A very robust form with a longer tube (3.5–6 mm) and with medium-sized flowers and sometimes very broad leaves (*G. wrightii*; *G. imbricata*, at least as to type).

3. A medium- to long-tubed form (5–8 mm) with large cream to pale yellow flowers and narrow to moderately broad leaves (*G. rubicunda*, *G. obtusata*).

4. A form similar to the previous but with a dark throat and often dark tube to the flower (*G. bicolor*).

It would seem convenient to give taxonomic recognition to all four forms or races as did Foster, but the existence of many intermediates, collected since Foster's monograph was published makes a revised treatment necessary. Lewis, in her treatment of *Geissorhiza* in the "Flora of the Cape Peninsula" (Lewis, 1950) maintained both the short-tubed form (as *G. imbricata*) and the

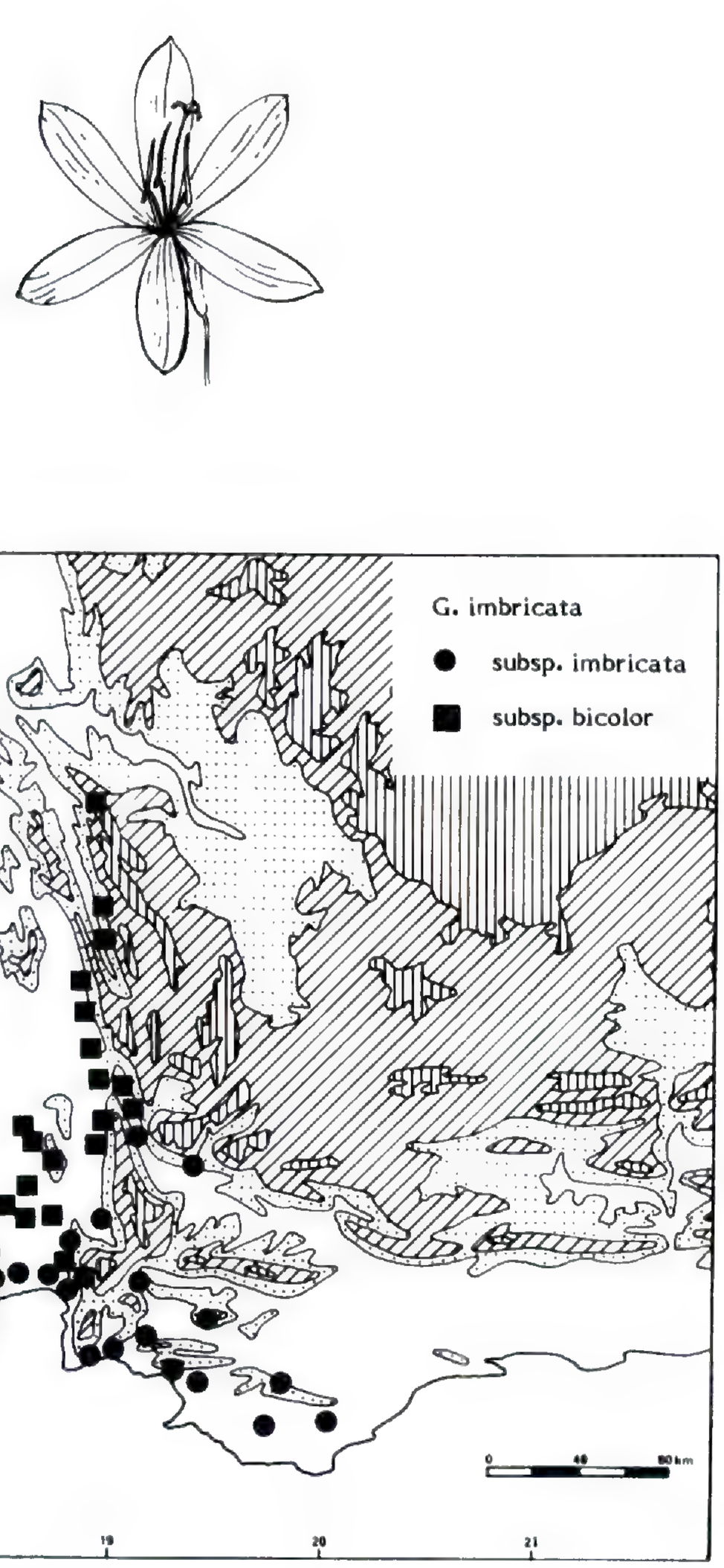


FIGURE 58. Morphology of *Geissorhiza imbricata* subspecies *imbricata* and the distribution of the two subspecies of *G. imbricata*. Habit ×0.5; flower life size; leaf section much enlarged (*Goldblatt s.n.* no voucher, Kirstenbosch).

robust and long-tubed *G. wrightii,* the only two forms occurring here, and most specimens on the Peninsula can readily be assigned to one of these. However, to the east in the Caledon and Bredasdorp districts a range of intermediates occur which I find impossible to assign with confidence to either of these taxa. The only solution seems to be to treat these as one taxon, which has in common small- to medium-sized flowers with a short to moderately long perianth tube. This taxon has a distinct southern distribution from the Cape Peninsula east to Bredasdorp.

It has also become impossible to continue to regard the cream- to pale yellow-flowered longer tubed forms with self-colored flowers as distinct from those with dark markings in the throat and tube. The difference here seems solely to be one of coloration and there are populations of plants with and without the dark color in the throat and tube.

However, at present it does seem useful to formally recognize this larger, cream- to yellow-flowered form with a generally longer perianth tube as a distinct taxon. The presence of intermediates between this and the shorter tubed, white-flowered form in the Worcester and Tulbagh districts that cannot be assigned with confidence to either form suggests that subspecific

status may be most appropriate. The cream- to yellow-flowered form is thus treated as *Geissorhiza imbricata* subsp. *bicolor* (Thunb.) Goldbl.

KEY TO THE SUBSPECIES OF *GEISSORHIZA IMBRICATA*

1a. Flowers white to cream (often red on the reverse of the outer tepals), without a dark center; perianth tube 2–4(–6) mm long; tepals 9–15(–17) mm long ..... subsp. *imbricata*

1b. Flowers cream to pale yellow (sometimes red on the reverse of the outer tepals), occasionally with a dark center; perianth tube (4–)5–8 mm long; tepals (16–)20–30 mm long ..... subsp. *bicolor*

50A. Subsp. imbricata. FIGURE 58.

Ixia scillaris Thunb., Diss. de *Ixia* no. 14. 1783, pro parte, hom. illeg. non L., excl. lectotype (Goldblatt, 1982).

Geissorhiza sabulosa Klatt, Trans. S. African Philos. Soc. 3: 203. 1885. TYPE: South Africa. Cape: near Camps Bay, *Templeman sub Macowan 2273* (lectotype, S, here designated; isolectotypes, K, SAM).

Geissorhiza wrightii Baker, J. Bot. n.s. 5: 238. 1876, Fl. Cap. 6: 69. 1896; Foster, Contr. Gray Herb. 135: 35–36. 1941; Lewis, Fl. Cape Penins. 255. 1950. TYPE: South Africa. Cape: Simons Bay, *Wright 243* [lectotype, K, designated by Foster (1941: 36); isolectotypes, G, L].

Geissorhiza sulphurea var. *arenicola* Foster, Contr. Gray Herb. 135: 37. 1941. TYPE: South Africa. Cape: Ceres Road (Wolseley), *Schlechter 8992* (holotype, B; isotypes, BM, BOL, BR, E, G, H, K, L, MO, PRE, S, Z).

Geissorhiza arenaria Ecklon ms. (*Ecklon 1597, 313*).

Plants (6–)10–20(–30) cm high. *Leaves* (1–)2–5(–10) mm wide. *Spike* (2–)6–8(–14)-flowered, flexed at the base and flexuose; *bracts* (6–)8–11 mm long. *Flower* stellate, white to cream, usually red on the reverse of the outer tepals; *perianth tube* 2–4(–6) mm long, enclosed in the bracts; *tepals* (9–)11–15(–17) mm long, obovate, (4.5–)5.5–7 mm wide, obtuse. *Filaments* (3–)4–5 mm long; *anthers* (3–)4–5 mm long, yellow. *Ovary* 2–3 mm long. *Capsule* oblong-globose, to 10 mm long. *Chromosome number*, $2n = 26$ (*Goldblatt 165*).

Flowering time. (August to) September to October.

Distribution. Cape Peninsula eastwards to the Caledon and Bredasdorp districts, and local in the Worcester district north to near Wolseley. Figure 58.

Geissorhiza wrightii was described by Baker in 1876 and although it has remained poorly understood, it has been consistently recognized ever since (Baker, 1896; Foster, 1941; Lewis, 1950). Foster actually saw little material of the species and was in some doubt about its status (Foster, 1941: 36) but he realized that it belonged to the "*imbricata* group." Lewis, who had a considerable field knowledge of Iridaceae, stated in "Flora of the Cape Peninsula" that it was very like *G. imbricata* but larger and more robust and with a longer perianth tube (Lewis, 1950). The key distinction she made was that the leaves of *G. imbricata* were 1–5 mm wide with the blade of the sheathing leaf about as long as the sheath, while the tepals were 9–20 mm long and the tube 1–2 mm long. In contrast, the leaves of *G. wrightii* were 5–8 mm wide with the blade of the sheathing leaf usually much longer than the sheath, while the tepals were 16–20 mm long and the tube 3–5 mm long.

The leaf blade versus the sheath distinction is poor and there are several collections in which specimens have blades either larger or shorter than the sheath (*Goldblatt 6189, Page s.n.*) while several narrow-leaved specimens have a blade much longer than the sheath (*Zeyher 1597*). Moreover, a few of the specimens determined by Lewis as *G. wrightii* have leaves less than 5 mm wide. It seems that like many species of the genus, *Geissorhiza imbricata* can be very variable as regards height; leaf width; and length, number, and size of the flowers. Accordingly, *G. wrightii* seems better regarded as merely robust *G. imbricata* subsp. *imbricata*, possibly genetically distinct, but equally likely, simply large due to good growing conditions. It is here regarded as taxonomically identical with *G. imbricata* and the less robust *G. sabulosa*.

Geissorhiza imbricata subsp. *imbricata* has a southern distribution from the Cape Peninsula and Cape Flats to Bredasdorp. To the north, it is replaced by the larger and cream- to yellow-flowered subsp. *bicolor* which grows in similar wet to semi-marshy places. In the Worcester district and around Stellenbosch where the two subspecies meet, it is often difficult to assign specimens with confidence to either and some populations seem completely intermediate between the two in some or all their characteristics. The differences between the two subspecies are dealt with in more detail under subsp. *bicolor*.

Specimens examined. SOUTH AFRICA. CAPE: 3318 (Cape Town) foot of Table Mt. near Kirstenbosch (CD), *H. Bolus 4710* (BM, BOL, K); foot of Table Mt., *MacOwan s.n. Herb. Norm. Austr. Afr. 258* (B, BM, G, GH, K); slopes near Blinkwater, *Levyns s.n.* (CT);

Camps Bay, *MacOwan 2273* (K, S, SAM), *Cassidy 287* (CT, SAM), *Lavranos 10993* (MO); above Camps Bay, *Wolley Dod 2767* (BOL, K), *Lewis 1213* (SAM), *Barker 3850* (NBG); Raapenberg, Mowbray, *Guthrie s.n.* (CT); Camp Ground, *Salter 9640* (BM); Kenilworth, *L. Bolus s.n.* (BOL 13944); Kenilworth Race Course, *Barker 4793* (NBG), *4114* (NBG), *Lewis 4793* (SAM), *Levyns s.n.* (CT 5889); Claremont, *Page s.n.* (BOL); Wynberg, damp fields, *H. Bolus s.n.* (BOL 31876); boggy ground, Fernwood, *Pillans 10640* (G, MO); Maitland flats, near cemetery, *Wolley Dod 2888* (BM, BOL, K); Stellenbosch flats (DD), *Strey s.n.* (M), *Garside 87* (K), *1049* (K).

3319 (Worcester) Ceres Road (Wolseley) (AC), *Schlechter 8992* (B, BM, BOL, E, G, H, K, L, MO, PRE, S, Z); Brandwacht, Worcester (CB), *Esterhuysen 8199* (BOL); Klein Drakenstein (CC), *Du Plessis s.n.* (STE 19731).

3418 (Simonstown) Schusterskraal vlei (AB), *Barker 3888* (BOL, NBG); marsh at Lakeside Station, *Salter 7034* (BOL); Modderdam, *Salter 8689* (BOL, CT, K, SAM); Constantiaberg, *Compton 15142* (NBG); lower slopes of Schoorsteenkop, Hout Bay, *Acocks 692* (PRE); Orange Kloof, in swamp, *Wolley Dod 3454* (BM, BOL, K); Three Beacons, Bergvliet flats, *Purcell s.n.* (MO, SAM 93340); Hout Bay, *Bond 1227* (NBG), *Compton 11295* (NBG); Constantia Nek, under pines, *Goldblatt 423* (BOL); Fish Hoek flats, *Salter 7397* (SAM); between Witsands and Redhill, *Lewis 1201* (BOL, SAM); Cape Flats (BA), *Zeyher s.n.* (SAM 20858), *Zeyher 1597* (B, BM, BOL, G, K, SAM, W, Z), *Pappe s.n.* (BM, SAM 20871), *Ecklon 313* (E, K, M, MO, P, S, Z), *Moss 4307* (Z), *4309* (BM); Cape Flats near the salt pans, *Bowie 12* (BM); near Sir Lowrys Pass Station (BB), *Diels 1252* (B); Faure, marshy ground, *van Niekerk 276* (BOL); Faure, *Barker 1824* (NBG), *2987* (NBG); Bettys Bay, wet soil (BD), *Ebersohn 358* (NBG).

3419 (Caledon) flats E of Viljoens Pass (AA), *Davis & Stokoe s.n.* (SAM 61719); Zwarteberg, Caledon (AB), *Templeman sub MacOwan 2611* (BOL, S, SAM); commonage at the foot of the Zwartberg, *Guthrie s.n.* (BOL 16919); wet area on Kleinmond road just S of Hermanus turnoff (AC), *Goldblatt 2989* (MO, PRE, WAG); Karwyderskraal, between Bot River and Hawston, *Lewis 5289* (NBG); Fernkloof Nature Reserve, Hermanus (AD), *Orchard 307* (BR, E, K, MO, WAG); Hermanus-Stanford road, wet recently burned ground, *Gillett 4166* (BOL), *4177* (BOL, K); kloof SW of Napier (BC), *Goldblatt 6189* (MO, NBG, PRE, S, US, WAG); wet flats near Franskraal (CB), *Goldblatt 7098* (MO, NBG, PRE); boggy ground near Elim (DA), *Muir 5019* (NBG); near The Poort, Bredasdorp (DB), *Barker 4594* (NBG), *Acocks 1526* (S).

WITHOUT PRECISE LOCALITY: *Thunberg s.n.* (S "Herb. Montin," Herb. Thunb. 993 UPS), Herb. Burman *s.n.* (G), *Oldenburg 45* (BM), *629* "*Ixia virginea*" (BM).

50B. Subsp. bicolor (Thunb.) Goldbl., comb. et stat. nov. *Ixia bicolor* Thunb., Phytogr. Blätt. 1: 3. 1803. *Geissorhiza bicolor* (Thunb.) N. E. Brown, J. Linn. Soc., Bot. 48: 44. 1928; Foster, Contr. Gray Herb. 135: 32–33. 1941. TYPE: South Africa. Cape: without precise locality, *Thunberg s.n.* "*Ixia bicolor α*" [lectotype, Herb. Thunb. 921 UPS, effectively designated by Brown (1928)]; "*Ixia bicolor β*" (syntype, Herb. Thunb. 922 UPS).

Geissorhiza obtusata Soland. ex Ker, Bot. Mag. 18: tab. 672. 1803. *Geissorhiza imbricata* var. *obtusata* (Ker) Baker, Fl. Cap. 6: 73. 1896. TYPE: South Africa. Cape: cultivated in England (originally collected by Niven) (illustration in Bot. Mag. tab. 672. 1803).

Geissorhiza imbricata var. *concolor* Baker, Fl. Cap. 6: 72. 1896; Foster, Contr. Gray Herb. 135: 38. 1941. TYPE: South Africa. Cape: near Somerset West, *H. Bolus 5567* [lectotype, K, designated by Foster (1941); isolectotype, BOL]; Somerset West, *Ecklon & Zeyher Irid. 111* (syntypes, B, G).

Geissorhiza rubicunda Foster, Contr. Gray Herb. 135: 35. 1941. TYPE: South Africa. Cape: Michells Pass, *Schlechter 8931* (holotype, B; isotypes, BM, BOL, BR, E, G, H, K, L, MO, P, PH, S, Z).

Geissorhiza bicolor var. *macowanii* Foster, Contr. Gray Herb. 135: 33. 1941. TYPE: South Africa. Cape: near Malmesbury, *MacOwan s.n. Herb. Norm. Austr. Afr. 1568* (holotype, G; isotypes, B, G, K, Z).

Geissorhiza aurea Ecklon, Topogr. Verz., Pflanzensamml. Ecklon 21. 1827 et ms. (*Ecklon & Zeyher Irid. 211*).

Plants 6–25 cm high. *Leaves* (1–)3–6(–9) mm wide. *Spike* 2–6(–9)-flowered, flexuose; *bracts* 10–12(–15) mm long. *Flower* somewhat cupped, cream to pale yellow, often red to purple-flushed on the reverse of the outer tepals, occasionally dark colored around the throat and then the tube usually also dark, rarely pale; *perianth tube* (4–)5–8 mm long, infundibuliform, usually slightly shorter than, or reaching the apex of the bracts, rarely exserted from the bracts; *tepals* (16–)20–30 mm long, obovate, 10–12 mm wide, obtuse. *Filaments* 7–10 mm long; *anthers* 5–7 mm long. *Ovary* 2.5–3.5 mm long. *Capsule* oblong to globose, 6–8 mm long. *Chromosome number,* unknown.

Flowering time. September to early October.

Distribution. Wet, usually sandy flats from False Bay north to Porterville, and in the Olifants River Valley. Figure 58.

Subspecies *bicolor* includes plants with pure yellow flowers as well as those with a dark center. Populations which have flowers with a dark center correspond closely to the type collection of *Geissorhiza bicolor* and are relatively rare, having been recorded from the Stellenbosch, Paarl, and Malmesbury districts, i.e., the south central part of the range of the subspecies. As far as I can tell all of the collections differ in no other character but the dark central color of the flower,

from the species known as *G. rubicunda* Foster. This was poorly known when first described but plants matching the type have now been collected at many sites in the Tulbagh and Porterville districts as well as in the Olifants River Valley to the north.

Collections matching *Geissorhiza bicolor* and *G. rubicunda* share the following significant features: a large pale yellow to cream, actinomorphic flower with tepals (16–)20–30 mm long; a relatively long perianth tube (4–)5–8 mm long, reaching nearly to the apex of or slightly exceeding the bracts; three usually fairly broad, several ribbed leaves; and spikes of up to 9, but usually 3–5 flowers. *Geissorhiza imbricata* subsp. *imbricata* typically has smaller white to cream flowers, with tepals 12–17 mm long, a short perianth tube 2.5–4(–6) mm long, not reaching the apex of the bracts, and fairly dense spikes of up to 12, but usually 6–8 flowers. The differences in flower size, color and, in particular, length of the perianth tube make confusion between most collections of these two subspecies unlikely.

Geissorhiza obtusata, Ker's "yellow flowered tile root," is included here in synonymy of subsp. *bicolor* as it seems to match almost perfectly *G. rubicunda.* The only type material known is the painting (tab. 672) in the "Botanical Magazine," the flowers of which are today either white (perhaps faded) or yellow in different copies of the volume. Baker (1896) treated this species as a variety of the related *G. imbricata.* Also included here in subsp. *bicolor* is *G. imbricata* var. *concolor* Baker (syn. *G. aurea* Ecklon nom. nud.) a distinct form from the southern Cape Flats. It has relatively broad and unusually obtuse leaves and self-colored flowers even lacking the usual red flush on the reverse of the tepals. *Geissorhiza bicolor* var. *macowanii* is apparently a name that Foster applied to a form with 3–4 flowers per spike and longer leaves than the two other collections which he assigned to *G. bicolor,* and it too is placed in synonymy.

Subspecies *bicolor* is closely related to the southwestern Cape species *G. brehmii* (syn. *G. teretifolia*), and the two can be distinguished only in their vegetative characteristics. *Geissorhiza brehmii* is a semi-aquatic species with terete, somewhat succulent or inflated leaves which if sectioned or viewed carefully with a lens can be seen to have four narrow longitudinal grooves running the length of the blade. Often its lowermost leaf is much reduced, vestigial, or even absent while the uppermost leaf is largest and ribbed on the inflated sheath and also occasionally on the free upper part. Such specimens are especially difficult to separate from narrow-leaved individuals of subsp. *bicolor.* The white to creamy yellow flowers of *G. brehmii* also occasionally have a dark center. The differences between subsp. *bicolor* and *G. brehmii* are consistent and it seems useful to continue to recognize the latter as a distinct species.

Geissorhiza imbricata subsp. *bicolor* is also sometimes confused with *G. purpureolutea.* This species has narrow two-grooved leaves, usually ca. 15 mm wide and a smaller flower with tepals 10–17(–22) mm long and a short perianth tube, 2–4 mm long. The plants are also usually short, 6–12 cm high, although they may reach 17 mm. The two species grow in the same habitat and occasionally close to one another.

Specimens examined. SOUTH AFRICA. CAPE: 3218 (Clanwilliam) Pakhuis Mt., Clanwilliam (BB), *MacOwan s.n. in Herb. Norm. Austr. Afr. 1969* (B, BM, G, GH, K, S, SAM, Z), *MacOwan 3328* (S, SAM).

3219 (Wuppertal) Platkloof, Citrusdal (CA), *Hanekom 1241* (K, PRE).

3318 (Cape Town) near Mamre (AD-BC), *MacOwan 2488* (K, SAM); Porterville (BB), *Loubser 485* (NBG), *401* (BOL); Twenty Four Rivers, damp slope near road bridge, *Goldblatt 6409* (K, MO, NBG, S); Twenty Four Streams, near Saron, *Lewis s.n.* (BOL 31877); damp places near Malmesbury, 120 m (BC), *Schlechter 1625* (B, BOL, BR, L, PRE, Z); hills near Malmesbury, 300 m, *Schlechter 1656* (BR, L, Z); near Malmesbury, *MacOwan s.n. Herb. Norm. Austr. Afr. 1568* (B, G, K, Z); N of Hermon, in clayish sand, *Goldblatt 6410* (MO); Kalabas Kraal (DA), *Barker 2543* (NBG); Paardeberg (DB), *Salter 7663* (SAM); near Durbanville (DC), *Compton 16016* (BOL, NBG); flats between Durbanville and Phesantekraal, *Leighton 557* (BOL); Bottelary road, near Stellenbosch (DD), *Lewis 2232 & Davis* (SAM); near Stellenbosch, *L. Bolus s.n.* (BOL); slopes of the Bottelary hills, *Acocks 3703A* (S); Stellenbosch Golf Course, *Bos 659* (STE, WAG); Stellenbosch Flats, *Garside 87* (K), *1050* (K).

3319 (Worcester) Saron, sandy flats (AA), *Lewis 5736* (NBG), *Martin s.n.* (NBG 60409); De Hoek Estates, near Saron, *Lewis s.n.* (BOL 31878); foot of Elandskloof Mts., Elandsrivier Farm (AC), *Goldblatt 5856* (MO); Commonage at Gouda, damp depressions, *Goldblatt 4214* (MO); Steendal, Tulbagh, *Pappe s.n.* (BOL); Wolseley, *Loubser 475* (NBG); Michells Pass, 1,500 ft. (AD), *Schlechter 8931* (B, BM, BOL, G, H, K, L, MO, PH, S, Z); Breede River flats near Worcester (CB), *Goldblatt 6982* (MO).

3418 (Simonstown) near Somerset West (BB), *Ecklon & Zeyher Irid. 211* (83) (B, BM, FI, K, MO, SAM); low lying fields, Somerset West, *H. Bolus 5567* (BOL, K); Vergelegen, swamp, *Lewis 5672* (NBG, STE); Faure, *van Niekerk 276* (BOL).

WITHOUT PRECISE LOCALITY: *Harvey 873* (E), *880* (E), *Thunberg s.n.* (Herb. Thunb. 991, 992, 961, UPS); between Piketberg and Piketberg Road Station, *H. Bo-*

lus s.n. (BOL), *Masson s.n.* "*Ixia obtusata* B" (BM), *s.n.* "*Ixia graminea* J. B." (BM), *Roxburgh s.n.* (BM "*Ixia obtusata* B," G).

51. Geissorhiza purpureolutea Baker, J. Bot. n.s. 5: 238. 1876, Fl. Cap. 6: 68. 1896; Foster, Contr. Gray Herb. 135: 33–34. 1941. TYPE: South Africa. Cape: between Paarl and Pont, *Drège 8476* [lectotype, K, effectively designated by Foster (1941); isolectotypes, G, L]. FIGURES 9, 59.

Geissorhiza sulphurea Schltr., Bot. Jahrb. Syst. 27: 99. 1899; Foster, Contr. Gray Herb. 135: 36–37. 1941 excl. var. *arenicola*. TYPE: South Africa. Cape: damp places near Ceres Road (Wolseley), *Schlechter 8981* [lectotype, B, effectively designated by Foster (1941); isolectotypes, BM, BOL, BR, E, G, H, K, MO, P, PH, PRE, S, Z].

Plants (4–)6–12(–17) cm high. *Corm* globose, more or less symmetric, 5–7 mm diam., tunics blackish, imbricate, regularly notched below into segments. *Cataphyll* not evident. *Leaves* 3, linear to narrowly ensiform, 1–2.5 mm wide, half as long to rarely as long as the stem, the margins and midrib strongly thickened, 2-grooved on each surface, more rarely 4 to several ribbed and grooved, the lower two leaves basal, the uppermost leaf largest, inserted near the base or on the lower part of the stem, sheathing the stem below for half its length, sheath inflated and strongly ribbed. *Stem* erect, simple. *Spike* 1–3(–5)-flowered, flexuose; *bracts* herbaceous, usually red-flushed near the apex, sometimes dry in the upper half at flowering time, 7–8 mm long. *Flowers* stellate, cream to pale yellow, usually intense brown (to purple) in the basal third of the tepals and tube, rarely self-colored, often reddish on the reverse of the outer tepals; *perianth tube* (2–)3–4 mm long, infundibuliform, usually about half as long as the bracts; *tepals* 10–17(–22) mm long, obovate 7–8 mm wide. *Filaments* equal, 5–6 mm long, often dark in the lower half; *anthers* 4–6 mm long, yellow. *Ovary* 2–3 mm long, *style* dividing near the apex of the anthers, branches ca. 2.5 mm long, recurved. *Capsule* unknown. *Chromosome number*, unknown.

Flowering time. Mid-August to mid-September.

Distribution. Wet, sandy gravel flats, on the coastal plain between Paarl and Piketberg and in the Tulbagh Valley. Figure 59.

Geissorhiza purpureolutea is a rare species of damp, poorly drained flats in the southwestern Cape. Its main range is the coastal lowlands between Paarl and Piketberg but it also occurs in the upper Tulbagh Valley, to the interior. Typical *G. purpureolutea* has moderate-sized cream to yellow flowers with a dark brown to purple center. In a collection from west of Malmesbury (*Lewis & Davis 2233*) several plants have either a typical or much reduced marking or it may be lacking. A second collection from this same general area in the west of the range of the species, *Salter 4756*, consists mostly of plants lacking markings entirely (one plant has a dark throat), but in all other respects match the Lewis and Davis collection, as well as some other collections (e.g., *Loubser 2034* from Piketberg) which have flowers slightly on the small side for the species.

These specimens that lack the central contrasting blotch match very closely collections in the Wolseley-Romans River area in the lower Tulbagh Valley, amongst which is *Schlechter 8981*, the type collection of *Geissorhiza sulphurea*. The Schlechter collection itself consists of rather small-flowered plants (tepals ca. 10 mm long), but the other collections from here (*Salter 6836, Goldblatt 2432*), have flowers of the same size (tepals 12–15 mm long) as typical *G. purpureolutea*. It seems likely that these collections represent nothing more than self-colored *G. purpureolutea*, and accordingly *G. sulphurea* is reduced to synonymy here.

Geissorhiza purpureolutea is closely allied to the *G. imbricata* complex from which it can usually be distinguished by its shorter perianth tube, 2–4 mm long, comparatively small flowers with tepals 10–17(–22) mm long, usually with a large central blotch of dark color, spikes of 1–3(–5) flowers and narrow basal leaves to 2.5 mm wide and usually 2 (rarely 4 to several) grooved.

A collection from the Darling area (*Lotter s.n.*) represents an unusual form of *Geissorhiza purpureolutea*. Plants have broad, several grooved leaves, and large flowers (tepals 20–22 mm long) with the typically short perianth tube of the species. The spikes have three or four flowers each. These plants are taken to be an extremely robust form of *G. purpureolutea*, rather than a separate taxon.

Specimens examined. SOUTH AFRICA. CAPE: 3218 (Clanwilliam) ca. 10 mi. N of Piketberg (DD), *Loubser 2034* (NBG); foot of Zebrakop, S of Eendekuil turnoff in gravelly soil, *Goldblatt 6129* (MO, NBG).

3318 (Cape Town) 18 mi. from Malmesbury on Hopefield road, damp ground (BA), *Lewis & Davis s.n.*

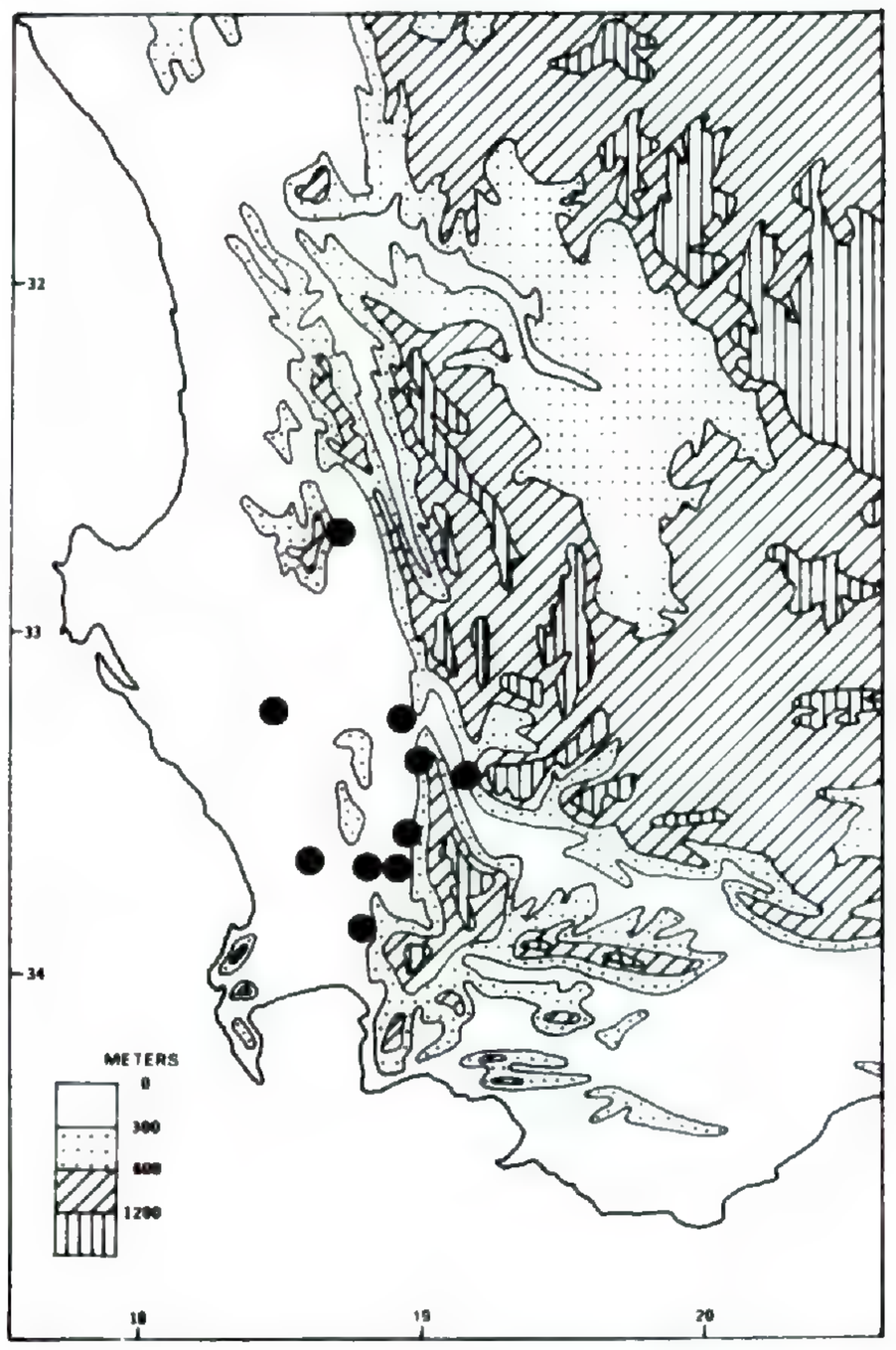


FIGURE 59. Morphology and distribution of *Geissorhiza purpureolutea*. Habit ×0.5; flower life size; leaf section much enlarged (*Goldblatt 6129*, foot of Zebrakop).

(PRE, SAM 60696); Oudepost, *Salter 4756* (BM, BOL, K); Spieka, near Klipheuwel, flats near river (DA), *Thompson 2613* (PRE, STE); near Wellington (DB), *L. Bolus s.n.* (BOL 20327, K, PRE), *Compton 11731* (NBG), *Barker 408* (NBG); near Paarl, *Barker 5948* (NBG); Paarl flats, N end, *Esterhuysen 6125* (BOL); between Paarl and Pont, *Drège 8475* (G, L), *8476* (G, K, L); flats N of Paarl, *Leighton 1960* (PRE); Huguenot, *Compton 18257* (NBG); ? near Stellenbosch (DD), *Edwards s.n.* (BOL).

3319 (Worcester) Gouda commonage, heavy clay soil (AC), *Goldblatt 2432A* (K, MO, PRE); Ceres Road (Wolseley), 700 ft., *Schlechter 8981* (B, BM, BOL, E, G, H, K, MO, P, PH, PRE, S, Z); between Darling Bridge and Romans River Siding, *Salter 6836* (BOL); flats between Bains Kloof and Wolseley, *Goldblatt 2432* (MO, PRE, US); Elandsberg farm, S of Gouda, *Goldblatt 6209* (MO).

52. Geissorhiza barkerae Goldbl., sp. nov. TYPE: South Africa. Cape: N of Piketberg, wet sites at the foot of Zebrakop, *Goldblatt 6391* (holotype, MO; isotypes, K, NBG, PRE, S, WAG). FIGURES 8, 60.

Planta 10–20 cm alta, foliis 3 inferioribus duobus basalibus lineari-ensiformibus marginibus costisque incrassatis, superiore infra inflato et vaginante, caule erecto saepe simplici, spica 2–4(–10) florum, floribus zygomorphis flavis atropurpureis insignis, tubo perianthii 7–8 mm longo, tepalis 22–30 mm longis, filamentis inaequalibus declinatis 15–20 mm longis, uno 5–6 mm breviore quam aliis, antheris 5–6 mm longis.

Plants 10–20 cm high. *Corm* globose, more or less symmetric, 7–11 mm diam., tunics blackish, imbricate, regularly notched below into segments. *Cataphyll* not evident. *Leaves* 3, linear (to ensiform), 1–4 mm wide, (2 to) 4 to several ribbed on each surface, about as long as the stem, the lower two basal, the uppermost largest, inserted near the base or in the lower part of the stem, sheathing the stem for half its length, the sheath inflated and strongly ribbed. *Stem* erect, usually 1-branched, flexed above the sheath of the upper leaf. *Spike* (2–)4–10-flowered, flexuose; *bracts* herbaceous, the upper margins hyaline, becoming dry and usually red-flushed near the apex, sometimes dry above at flowering time, 10–13 mm long. *Flowers* zygomorphic, with the style and stamens declinate and held above the nearly horizontal upper tepal, pale yellow marked with purple in the lower half of the tepals and yellow in the center and tube, often reddish on the reverse of the outer tepals; *perianth tube* 7–8 mm long, infundibuliform; *tepals* 22–30 mm long, lanceolate, 8–9 mm wide. *Filaments* unequal, two longer, 15–20 mm, the shorter, 10–14 mm long, yellow; *anthers* 5–6 mm long, yel-

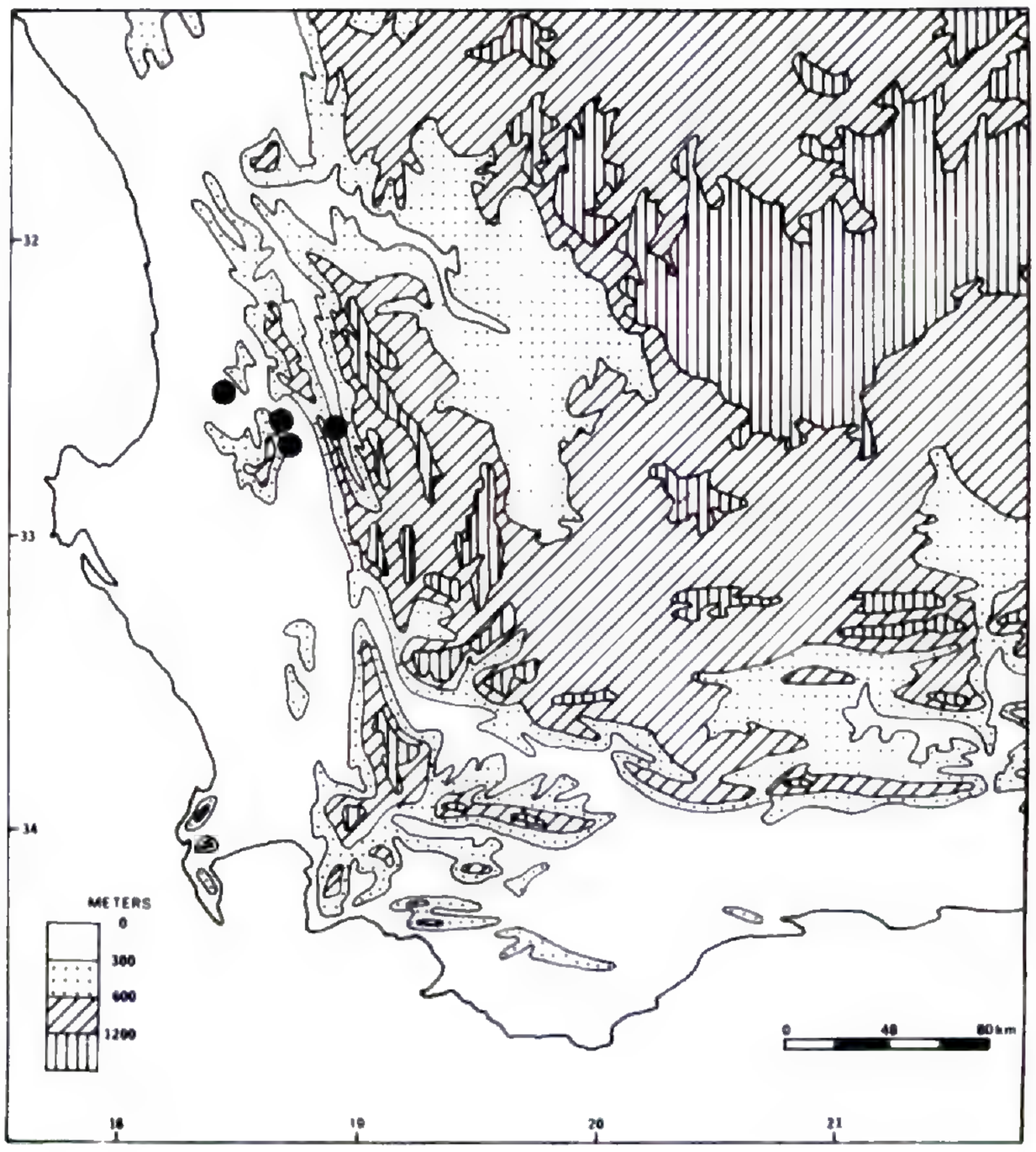


FIGURE 60. Morphology and distribution of *Geissorhiza barkerae*. Habit ×0.5; flower life size; leaf section much enlarged (*Goldblatt 6391*, foot of Zebrakop).

low. *Ovary* ca. 2–3 mm long, *style* dividing near the apex of the anthers, branches ca. 5 mm long, recurved. *Capsule* unknown. *Chromosome number*, $2n = 26$ (*Goldblatt 6391*).

Flowering time. Mid-September to mid-October.

Distribution. Seasonal marshes and stream banks in sand or light clay north and northwest of Piketberg, and locally in the Olifants River Valley. Figure 60.

Geissorhiza barkerae is a very distinctive species, with a local distribution, north and west of Piketberg, where it grows in seasonally flooded or waterlogged sandy or light clay soils. It is allied to *G. imbricata* especially subsp. *bicolor* which occurs in similar habitats to the south and to *G. louisabolusiae* which occurs in the Olifants River Valley to the north. It can readily be distinguished from these two species by its large, zygomorphic flowers borne on drooping spikes of up to ten flowers. The flowers are pale yellow with dark purple in the lower part of the tepals while the throat and tube are also yellow. The stamens are declinate and very unequal, with the two longer filaments 15–20 mm long and the

shorter one about two-thirds this length. In contrast, *G. imbricata* subsp. *bicolor* has somewhat smaller and actinomorphic flowers sometimes with a dark center, and then usually a dark perianth tube (not so in the type). It also has fewer flowers in a spike (2–5, rarely to 10), and equal filaments. *Geissorhiza louisabolusiae* has self-colored, and smaller, deeper yellow flowers with a shorter perianth tube, and subequal to slightly unequal filaments, and typically much narrower, linear, 2-grooved leaves.

I have pleasure in naming this species in honor of W. F. Barker, the South African botanist, and retired Curator of the Compton Herbarium, Kirstenbosch. Her extensive collecting over many years has been of great value, particularly as she has taken great care in preparation of her specimens, thus making many characters easy to see which would otherwise be lost, and thus require recollecting.

Specimens examined. SOUTH AFRICA. CAPE: 3218 (Clanwilliam) Papkuils Vlei (CB), *Leighton 121* (BOL, PRE), *Compton 9502* (NBG, W), *Barker 2639* (BOL, NBG); Vogelvlei, near Eendekuil (DB), *Marloth 9247* (PRE); flats at foot of Zebrakop, S of Concordia farm, *Goldblatt 6391* (K, MO, NBG, PRE, S, WAG); N of Piketberg, wet ground along road to Het Kruis, *Goldblatt 542* (BOL).

3219 (Wuppertal) Warm Baths, Clanwilliam (CA), *Leipoldt s.n.* (BOL 31881, K).

WITHOUT PRECISE LOCALITY: Sandveld between Greys Pass and Graafwater, *Leipoldt 3585* (BOL); Cape Town Wild Flower Show, Oct. 1939, *Anon.* (BOL 31880); "Tulbagh," *Thom s.n.* (K).

53. Geissorhiza louisabolusiae Foster, Contr. Gray Herb. 135: 34. 1941, pro parte excl. var. *longifolia*. TYPE: South Africa. Cape: 6 mi. E of Graafwater, *Salter 2790* (holotype, K; isotypes, BM, BOL). FIGURE 61.

Plants (10–)15–20 cm high. *Corm* globose, 7–9 mm diam., symmetric, tunics blackish, imbricate, notched into regular segments below. *Cataphyll* not evident. *Leaves* 3, linear to nearly terete, 1–2 mm wide, reaching to about the base of the spike, narrowly 4–6(–8)-grooved on each surface, the lower two leaves basal, the uppermost basal or inserted shortly above the ground and largest, sheathing the stem below, the sheath ribbed and inflated. *Stem* erect, sheathed for half to two-thirds its length, flexed above the sheath, occasionally with 1 branch. *Spike* flexuose, inclined (2–)3–7-flowered; *bracts* herbaceous, occasionally the margin lined red above, often becoming dry and membranous from the apex, 8–10 mm long, the inner shorter than the outer. *Flower* actinomorphic, the tepals somewhat cupped, bright yellow; *perianth tube* 4–6 mm long, nearly reaching the apex of the bracts (exserted in old blooms), infundibuliform; *tepals* 18–28 mm long, 7–9 mm wide, oval. *Filaments* nearly equal to unequal, longer two 7–9 mm long, the third if shorter, 5–7 mm long; *anthers* 4.5–6 mm long, yellow. *Ovary* ca. 2–3 mm long, *style* dividing near the apex of the anthers, branches ca. 2 mm long, recurved. *Capsule* unknown. *Chromosome number*, $2n = 26$ (*Goldblatt 427*).

Flowering time. Late August to September.

Distribution. Damp often waterlogged sand or shallow vleis, in the Olifants River Valley and valleys of the Olifants River Mountains to the west. Figure 61.

Geissorhiza louisabolusiae has a limited distribution, occurring in the Olifants River Valley and the adjacent valleys of the Olifants River Mountains to the west. It is restricted to wet sandy flats and vleis that are waterlogged in the late winter and spring. This habitat is now becoming much reduced owing to the expanding citrus and deciduous fruit orchards that have been developed in this area, and *G. louisabolusiae* is, as a result, rapidly becoming endangered.

It appears to be a member of the *G. imbricata* group and although it does not have the corrugated leaves typical of the alliance, the sheathing part of the upper leaf is characteristically ribbed and grooved. It appears to be most closely related to the southwestern Cape species *G. brehmii* (syn. *G. teretifolia*) but it can readily be distinguished from this species. *Geissorhiza louisabolusiae* has deep yellow flowers with a relatively short perianth tube, 4–6 mm long, a flower with ascending somewhat cupped tepals, and usually one stamen slightly to appreciably shorter than the others. In contrast, *G. brehmii* usually has a longer perianth tube, 5–9 mm long, either white, cream, or pale yellow flowers, sometimes with a dark center and equal stamens. The leaves of *G. louisabolusiae* are more or less terete and narrowly 4–6(–8)-grooved, with the two basal equally well-developed, while those of *G. brehmii* are fully terete and inflated, always 4-grooved and the lowermost of the basal leaves is much smaller than the other, sometimes being vestigial or even absent.

The variety *Geissorhiza louisabolusiae* var. *longifolia* recognized by Foster (1941), based on a Bachmann collection from near Moorreesburg

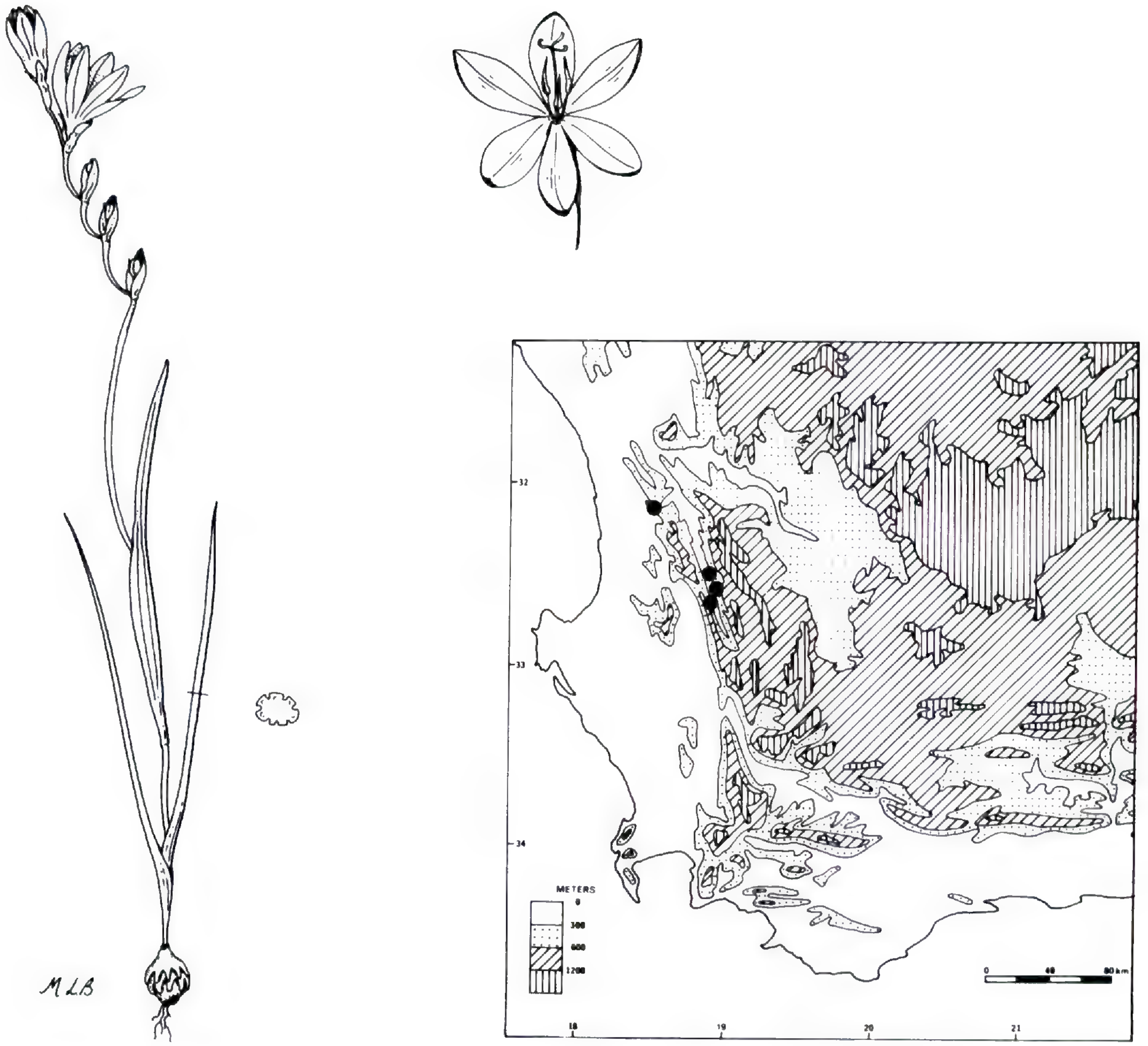


FIGURE 61. Morphology and distribution of *Geissorhiza louisabolusiae*. Habit ×0.5; flower life size; leaf section much enlarged (*Goldblatt 6268*, flats N of Citrusdal).

is here referred to *Geissorhiza brehmii*. It appears to be no more than a robust form of this species but quite characteristic in its long perianth tube, inflated terete leaves, and much reduced or lacking lowermost leaf.

Specimens examined. SOUTH AFRICA. CAPE: 3218 (Clanwilliam) 6 mi. E of Graafwater (BA), *Salter 2790* (BM, BOL, K).

3318 (Wuppertal) Citrusdal (CA), *Barker 7343* (NBG), *3078* (BOL, NBG), *Leighton 1090* (BOL); flats N of Citrusdal, *Salter 3659* (BM, BOL, K), *Goldblatt 247* (BOL), *Goldblatt 6268* (MO); 5 mi. N of Citrusdal, *Lewis 1416* (SAM); Citrusdal vlei, *Barker 3604* (NBG); Warm Baths, Olifants River Valley, *Leipoldt s.n.* (BOL 31879); Leeu River bridge, growing in vlei (CC), *Horrocks 32* (NBG).

54. Geissorhiza brehmii Ecklon ex Klatt, Linnaea 34: 653–654. 1866. *Geissorhiza imbricata* var. *brehmii* (Klatt) Foster, Contr. Gray Herb. 135: 38. 1941. TYPE: South Africa. Cape: Hottentots Holland, about Somerset West, *Ecklon & Zeyher Irid. 295* (83) [lectotype, B, effectively designated by Foster (1941: 38); isolectotypes, FI, G]; Cape, about Somerset West, *Ecklon & Zeyher Irid. 211* "*G. aurea*" [syntypes, B, FI, MO, SAM = *G. bicolor* (Thunb.) N. E. Brown sensu lato].

Geissorhiza louisabolusii var. *longifolia* Foster, Contr. Gray Herb. 135: 34. 1941. TYPE: South Africa. Cape: road to Mooreesburg, Malmesbury, *Bachmann 1091* (holotype, B; isotype, Z).

Geissorhiza teretifolia Lewis, J. S. African Bot. 7: 48. 1941. TYPE: South Africa. Cape: Kenilworth Race Course, *Lewis 97* (holotype, SAM 53064).

Plants 20–30 cm high. *Corm* 8–12 mm diam., globose, tunics blackish, imbricate, the outer lay-

ers accumulating above, regularly notched below into triangular segments. *Cataphyll* single, extending shortly above ground, firm membranous. *Leaves* 2 or 3, usually terete and inflated or somewhat succulent with 4 very narrow longitudinal grooves running the length of the leaf, the lower one or two basal, the lowermost small, often broken, or vestigial (occasionally lacking), the second about as long as the stem, the uppermost usually inserted on the stem shortly above the ground, sheathing below, the sheath ribbed and inflated, the free upper part often as long as the basal leaf (or leaves), terete or occasionally ribbed. *Stem* erect, often branched. *Spike* 2–6-flowered, flexuose; *bracts* herbaceous, becoming dry and membranous from the apex, 7–10 (–15) mm long, the inner smaller than the outer. *Flower* more or less stellate, white to cream, sometimes purple-flushed on the reverse of outer tepals, occasionally dark colored in the throat and tube; *perianth tube* 5–7(–9) mm long, slightly shorter than, or reaching the apex of the bracts; *tepals* 15–20(–26) mm long to 9 mm wide, obovate, obtuse. *Filaments* 5–9 mm long, equal; *anthers* ca. 5 mm long. *Ovary* ca. 2 mm long, *style* dividing near the apex of the anthers, branches 3–4 mm long, recurved. *Capsule* unknown. *Chromosome number,* unknown.

Flowering time. (August to) September to October.

Distribution. Cape Peninsula, north to the Malmesbury district and east to Caledon and Bredasdorp in sandy ground, either swampy, or seasonally flooded, or at edges of pools. Figure 62.

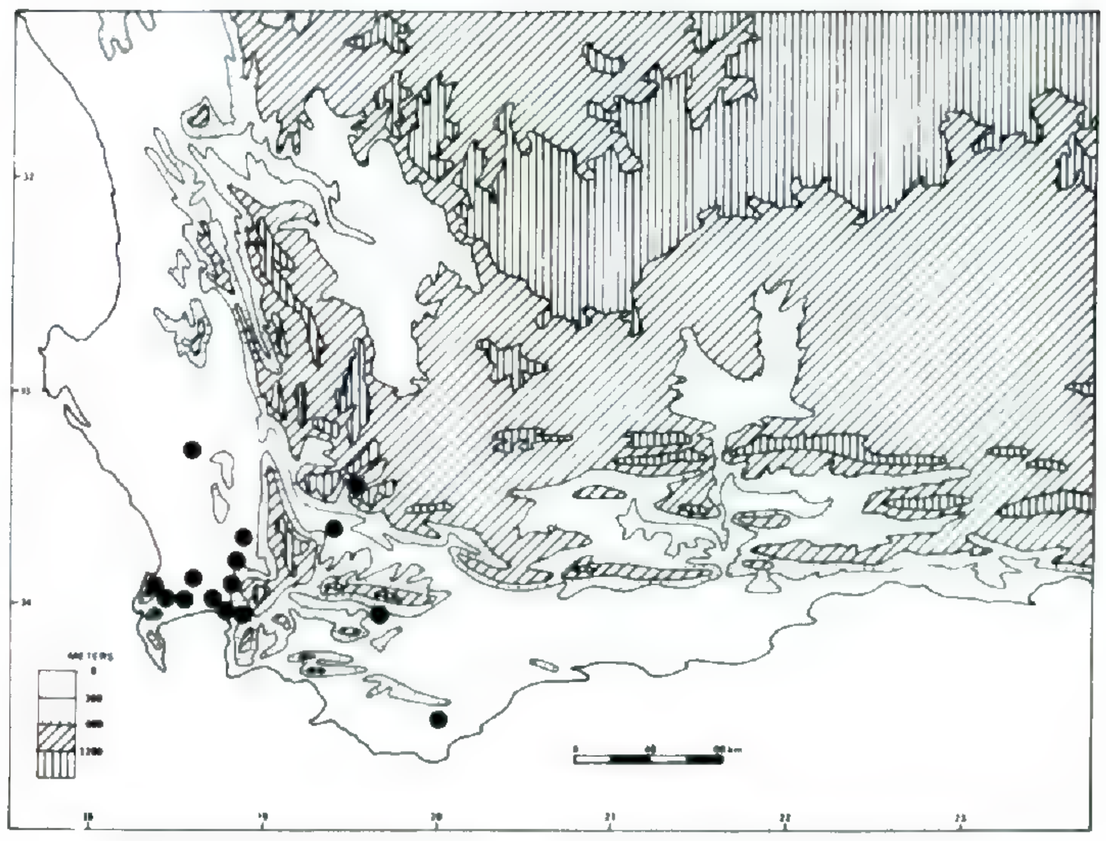


FIGURE 62. Distribution of *Geissorhiza brehmii.*

Geissorhiza brehmii is closely related to *G. imbricata* especially to subsp. *bicolor* (here including *G. rubicunda*) and the two taxa have a similar general appearance and flower. *Geissorhiza brehmii* grows in wetter habitats, usually in standing water, or in sites usually flooded in the winter, but sometimes nearly dry by flowering time. It can be distinguished by its habitat and otherwise only in its vegetative characteristics, by its slender terete and slightly succulent, narrowly 4-grooved leaf, the lowermost of which is often much smaller than the others, or even vestigial or lacking. *Geissorhiza imbricata* has in contrast linear to ensiform, several ribbed, flat leaves, the lower of which is always well developed. Occasional narrow-leaved individuals of *G. imbricata* subsp. *bicolor* are encountered (e.g., *Goldblatt 6409*) but leaves of these plants are not terete or inflated and can be seen under a lens to be 1–2-ribbed on each surface. In some collections of *G. brehmii* one or a few plants may have ribbed leaves (e.g., *Compton 20095*), and it becomes very difficult to distinguish such specimens from subsp. *bicolor.*

As published, *Geissorhiza brehmii* appears to be a superfluous name for Klatt (1866) who cited two apparent synonyms in the protologue, "*G. setacea* Gawl." and "*G. aurea* Ecklon." However, Klatt was almost certainly citing *G. setacea* in reference to the "Botanical Magazine" fig. 1255 which Ker (Ker-Gawler) identified as *G. setacea* although in fact it is not this species, but probably *G. hispidula* (syn. *G. humilis* var. *hispidula* Foster). Klatt's intention seems to have been to draw attention to *G. setacea* sensu Ker as distinct from the true *G. setacea* based on the Thunberg type. The other name cited, *G. aurea* Ecklon, is a nomen nudum.

Klatt cited two collections in his description of *Geissorhiza brehmii,* both from near Somerset West, *Ecklon & Zeyher Irid. 295* (*G. brehmii* Ecklon ms.) and *Ecklon & Zeyher Irid. 211* (*G. aurea* Ecklon ms.). These are different species, the latter being a cream- to yellow-flowered form of *G. bicolor* with self-colored flowers and relatively broad leaves with obtuse apices. Foster effectively designated *Ecklon & Zeyher Irid. 295* as the lectotype for *G. brehmii* when he reduced it to varietal rank in *G. imbricata,* where it was distinguished by its narrow leaves. Lewis (1941) quite independently described *G. teretifolia* based on collections from the Cape Peninsula, before Foster's (1941) revision was published. *Geissorhiza teretifolia* differs in no significant way from *G. brehmii,* although the material cited by Lewis

is in general more robust than the lectotype of *G. brehmii* and has white flowers.

Most populations of *Geissorhiza brehmii* have white- to cream-colored flowers, with a faint pink flush on the reverse of the outer tepals. Plants from Mulders Vlei and Kraaifontein in the northern Cape Flats, however, apparently have cream flowers (yellow on drying) with a distinct red streak on the reverse of the outer tepals and a dark color in the throat and tube of the perianth. The Kraaifontein population (*Compton 20095*) comprises plants with either a dark, or self-colored throat and tube, while in the Mulders Vlei population (*Lewis 4447*) all plants have the dark color in the center of the flower. Some plants of this collection also have unusually large flowers, with tepals to 26 mm long and perianth tube to 9 mm. There seems no reason, however, to treat this form as a separate taxon.

Other large-flowered populations have been recorded, e.g., *Bachmann 1091* and *H. Bolus 4339*. Plants of these collections have apparently cream-colored flowers without any marking on the reverse of the tepals. These have either only one basal leaf, or at most a vestigial second basal leaf. The Bachmann collection is the type collection of Foster's *Geissorhiza louisabolusiae* var. *longifolia*. *Geissorhiza louisabolusiae* is in fact, superficially similar to *G. brehmii,* but always has two well-developed basal leaves, usually a shorter perianth tube, and subequal to unequal stamens. Differences between these two species, in leaf morphology and in the length of the perianth tube, make it easy to distinguish them. *Geissorhiza louisabolusiae* var. *longifolia* is here reduced to synonymy in *G. brehmii*.

Geissorhiza brehmii has been confused at times with *G. hispidula* (Klatt, 1866) and with *G. geminata* (Foster 1941: 78). Several collections of *G. hispidula* made by Ecklon and Zeyher bear the manuscript name *G. brehmii*. Both *G. hispidula* and *G. geminata* (subgenus *Weihea*) have concentric corm tunics and are unrelated to *G. brehmii,* which has imbricate tunics typical of subgenus *Geissorhiza*.

Specimens examined. SOUTH AFRICA. CAPE: 3318 (Cape Town) Hopefield district (?AB), *Bachmann 1090* (Z); road to Moorreesburg (?BA), *Bachmann 1091* (B, Z); Kenilworth Race Course, in pools (CD), *Lewis 4796* (PRE, SAM), *97* (SAM), *480* (SAM), *Barker 4795* (NBG), *4115* (NBG), *Salter 7738* (BM, BOL, CT, K, SAM), *Dümmer 724* (E); wet places on Table Mt., 2,300 ft., *Schlechter 92* (B, G, W); Kraaifontein (DC), *Compton 20095* (BOL, NBG, STE); Bergrivier at Paarl, "feuchten Wiesen und in Dümpfel" (DD), *Drège 8472* (B, BM, E, K, L, MO, P, S); Stellenbosch flats, *Holzapfel 6* (STE), *Garside 1063* (K); Old Golf Course, Stellenbosch, *Du Preez s.n.* (STE); Mulders Vlei, *Lewis 4447* (PRE, SAM).

3319 (Worcester) Hex River Valley (BC-CB), *Davidson 75* (SAM); between Worcester and Villiersdorp (CD), *Lewis 2899* (SAM), *2900* (SAM).

3418 (Simonstown) Ottery Road Station (AB), *Lewis 130* (SAM); Wynberg, *Wilms 3733* (B), *Schlechter 1557* (B, G, M, W, Z); Cape flats (BA), *Ecklon & Zeyher 427* (BOL, SAM); farm Vergenoeg, near Faure, damp sandy flats, *Thompson 2114* (PRE, STE); wet sandy flats between Gordon's Bay and Strand (BB), *Esterhuysen 23133*; Hottentots Holland, *Drège 8465* (S); near Somerset West, *Ecklon & Zeyher Irid. 295* (83) (B, FI, G).

3419 (Caledon) damp slopes and ditch, Lindeshof (BB), *Lewis 5658* (NBG, STE); The Poort, Bredasdorp, in swampy ground (DB), *Dymond s.n.* (BOL 21227), *Barker 2493* (NBG).

WITHOUT PRECISE LOCALITY: Cape of Good Hope, *Siebold 526* (B), *Ecklon s.n.* (PRE); Zonderend Mts., *Stokoe s.n.* (SAM 57388).

55. Geissorhiza sulphurascens Schltr. ex Foster, Contr. Gray Herb. 35: 39. 1941. TYPE: South Africa. Cape: Bokkeveld W of Nieuwoudtville, *Marloth 7658* (holotype, B; isotype, PRE). FIGURE 63.

Plants 12–20 cm high. *Corm* globose, 6–8 mm diam., symmetric, tunics blackish, imbricate, notched into regular segments below. *Cataphyll* not evident. *Leaves* 3, narrow, linear, ca. 1 mm wide, reaching the midline of the stem or the base of the spike, the margins and midrib enlarged and 2-grooved on each surface, the lower two leaves basal, the uppermost basal or inserted just above the ground, largest, sheathing the stem in its lower two-thirds, the sheath ribbed and inflated. *Stem* erect, sheathed below for about two-thirds its length, flexed above the sheath of the upper leaf, occasionally with 1 branch. *Spike* flexuose, inclined, 4–8(–10)-flowered; *bracts* herbaceous, the margin often lined red above, sometimes becoming dry and brownish from the apex, 7–9 mm long, the inner shorter than the outer. *Flower* stellate, or the tepals slightly cupped, cream; *perianth tube* 3–4 mm long, enclosed in the bracts, infundibuliform; *tepals* 13–18 mm long, 5–7 mm wide, oval. *Filaments* equal, 5–8 mm long; *anthers* ca. 6 mm long, pale yellow. *Ovary* ca. 2.5 mm long, *style* dividing at the apex of the anthers, branches ca. 2 mm long, recurved. *Capsule* more or less globose about 5 mm long. *Chromosome number,* unknown.

Flowering time. Late August to September.

Distribution. Nieuwoudtville Escarpment, in damp sand. Figure 63.

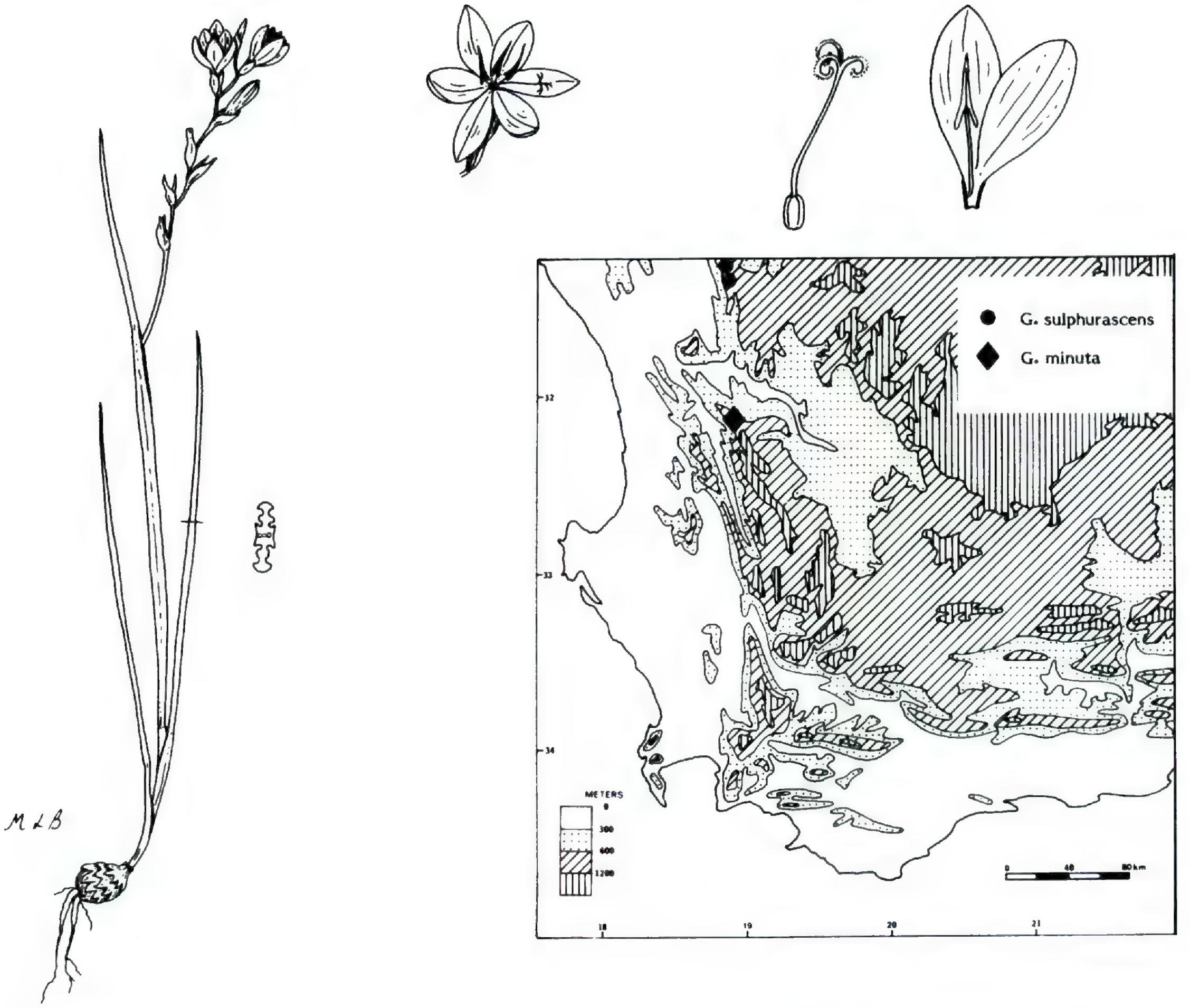


FIGURE 63. Morphology of *Geissorhiza sulphurascens* and distribution of *G. sulphurascens* and *G. minuta*. Habit ×0.5; flower life size; partial flower and gynoecium ×1.5; leaf section much enlarged (*Goldblatt 5841*, Grasberg road, Nieuwoudtville).

Geissorhiza sulphurascens is endemic to the Bokkeveld Escarpment where it is common in the Nieuwoudtville-Van Rhyns Pass area on poorly drained, wet, sandy sites. It is related to the *G. imbricata* group, the other species of which occur to the south from the Olifants River Valley to the Cape Peninsula and Bredasdorp. While it seems somewhat isolated taxonomically, it is perhaps most closely related to *G. louisabolusiae* a species with fewer and larger, bright yellow flowers on a lax inflorescence and typically unequal stamens. The pale creamy yellow flowers and congested inflorescence of *G. sulphurascens* are distinctive, as are the linear and 4-grooved basal leaves and well-developed uppermost leaf which sheaths at least two-thirds of the stem.

Specimens examined. SOUTH AFRICA. CAPE: 3119 (Calvinia) Nieuwoudtville Escarpment NW of Van Rhyns Pass (AC), *Oliver 3849* (K, PRE, STE); Nieuwoudtville, *L. Bolus s.n.* (PRE 36875), *Loubser 953* (NBG); Willemsrivier, *Leipoldt 720* (BOL, PRE); marshy soil near Nieuwoudtville, *Leipoldt 792* (BOL); Bokkeveld W of Nieuwoudtville, *Marloth 7658* (B, PRE); Grasberg road, NW of Nieuwoudtville, damp sandy soil, *Barker 9559* (NBG), *Goldblatt 5841* (MO, PRE, S); Meulsteenvlei, near edge of escarpment W of Nieuwoudtville, *Lewis 5870* (NBG); 4 km NW of Nieuwoudtville on Grasberg road, *Goldblatt 6218* (MO); 2 mi. W of Nieuwoudtville, *Hall 3874* (NBG); Uitkomst farm SW of Nieuwoudtville, in sand, *Barker 10740* (K, NBG).

56. Geissorhiza minuta Goldbl., sp. nov. TYPE: South Africa. Cape: Pakhuis Pass, *Esterhuysen 3193* (holotype, BOL; isotypes, K, MO).

Planta 3–8(–12) cm alta, tunicis cormi imbricatis, foliis 3, inferioribus duobus basalibus linearibus,

superiore caulem vaginante, caule erecto, spica 2–6 florum, floribus stellatis, albis, tubo ca. 1 mm longo, tepalis 7–8 mm longis, antheris 2–3 mm longis, stylo diviso prope apicem antherarum.

Plants 3–8(–12) cm high. *Corm* globose, 5–6 mm diam., symmetric, tunics blackish, imbricate, notched into regular segments below. *Cataphyll* not evident. *Leaves* 3, linear, ca. 1 mm wide, about as long as the spike, the margins and midrib enlarged and 2-grooved on each surface, the lower two leaves basal, the uppermost basal or inserted just above the ground, longer or shorter than the lower leaves, sheathing the stem in its lower two-thirds, the sheath ribbed and somewhat inflated. *Stem* erect, sheathed for about two-thirds its length, flexed above the sheath of the upper leaf, occasionally with 1 branch from the base. *Spike* flexuose, inclined, 2–6-flowered; *bracts* herbaceous, the upper margin often red, sometimes becoming dry and brownish from the apex, 4–5 mm long, the inner about as long as the outer. *Flower* evidently white, stellate; *perianth tube* ca. 1 mm long, enclosed in the bracts, infundibuliform; *tepals* 7–8 mm long, ca. 2.5 mm wide, oval. *Filaments* apparently equal, 2–3 mm long; *anthers* 2–3 mm long, pale yellow. *Ovary* ca. 1 mm long, *style* dividing just beyond the apex of the anthers, branches 1–1.5 mm long, recurved. *Capsule* unknown. *Chromosome number,* unknown.

Flowering time. September to early October.

Distribution. Moist, rocky places in the Pakhuis Mountains. Figure 63.

Geissorhiza minuta is a dwarf species of subgenus and section *Geissorhiza,* apparently most closely related to *G. sulphurascens,* an endemic of the Nieuwoudtville Plateau. *Geissorhiza minuta* has white flowers, which are amongst the smallest in the genus. Its short perianth tube, ca. 1 mm long, tepals 7–8 mm long, and short anthers, 2–3 mm long, as well as slender habit and dwarf stature make confusion with any other species unlikely. It has only been collected in the vicinity of Pakhuis Pass and is probably endemic to this limited area to the north of the main Cedarberg range.

Specimens examined. SOUTH AFRICA. CAPE: 3219 (Wuppertal) Pakhuis Pass, wet, mossy stones (AA), *Bond 675* (NBG); Pakhuis Pass, *Barker 4715* (NBG), *Lewis 1871* (SAM); Pakhuis Pass, moist spot among rocks, *Esterhuysen 3193* (BOL, MO).

57. Geissorhiza eurystigma L. Bolus, S. African Gard. 21: 282. 1931. *Geissorhiza mathewsii* var. *eurystigma* (L. Bolus) Foster, Contr. Gray Herb. 135: 27–28. 1941. TYPE: South Africa. Cape: near Mamre, *L. Bolus s.n.* (lectotype, BOL 19876, here designated; isolectotype, K). FIGURE 64.

Ixia secunda de la Roche, Diss. 17–18. 1766. *Geissorhiza monantha* Sweet, Hort. Brit. 2nd edition, 503. 1830, nom. nov. pro *Ixia secunda* de la Roche [*G. secunda* (Ker) Ker, 1804 bars transfer to *Geissorhiza* and treated here as a synonym of *G. monanthos* Ecklon, 1827 after Articles 64.2 and 75 of the Botanical Code of Nomenclature]. TYPE: South Africa. Cape: without precise locality, *Anon. s.n.* "*Ixia secunda* La Roche" (holotype, L).

Ixia rochensis Ker non sensu Ker, Bot. Mag. 17: tab. 598. 1802, nom. illeg. superfl. pro *I. secunda* de la Roche (misapplied to *G. radians*).

Geissorhiza rochensis (Ker) Ker, Ann. Bot. (König & Sims) 1: 221. 1804, nom. illeg. basion. illeg. superfl. (misapplied to *G. radians*).

Geissorhiza rochensis var. *monantha* (Sweet) Baker non sensu Baker, Handb. Irid. 156. 1892, Fl. Cap. 6: 71. 1896 (misapplied to *G. monanthos* Ecklon).

Ixia rochensis var. *spithamaea* Ker, Bot. Mag. 17: tab. 598. 1802. *Geissorhiza rochensis* var. *spithamaea* (Ker) Baker, Handb. Irid. 156. 1892, Fl. Cap. 6: 71. 1896, pro parte; Foster, Contr. Gray Herb. 135: 29–30. 1941, pro parte. TYPE: South Africa. Cape: precise locality unknown, *Masson s.n.* "*Ixia violacea*" (lectotype, BM, here designated).

Plants 8–15(–20) cm high. *Corm* globose, more or less symmetric, 8–11 mm diam., truncate at the base, tunics imbricate, blackish, layers notched below into regular segments. *Cataphyll* membranous or evidently lacking. *Leaves* 3, ensiform, conspicuously several ribbed, reaching to the base or middle of the spike, 3–6 mm wide, the lower two leaves basal, the uppermost inserted at the base or in the lower part of the stem, sheathing and inflated below, often as long and larger than the lower leaves. *Stem* flexed above sheath of the upper leaf and at the base of the spike, rarely bearing a bract-like leaf in the upper half, simple or 1–2-branched. *Spike* flexuose (1–)2–5(–7)-flowered; *bracts* herbaceous, green, becoming dry and membranous from the apex and often reddish on the upper margin, 9–13 mm long, the inner about as long as the outer but narrower. *Flowers* evidently actinomorphic, the tepals widely cupped, dark blue with a red center; *perianth tube* fairly long, and widening gradually from the base, 6–9 mm long, exserted from the bracts; *tepals* 16–24 mm long, 9–13 mm wide, obovate, blue above, red in the lower half. *Fil-*

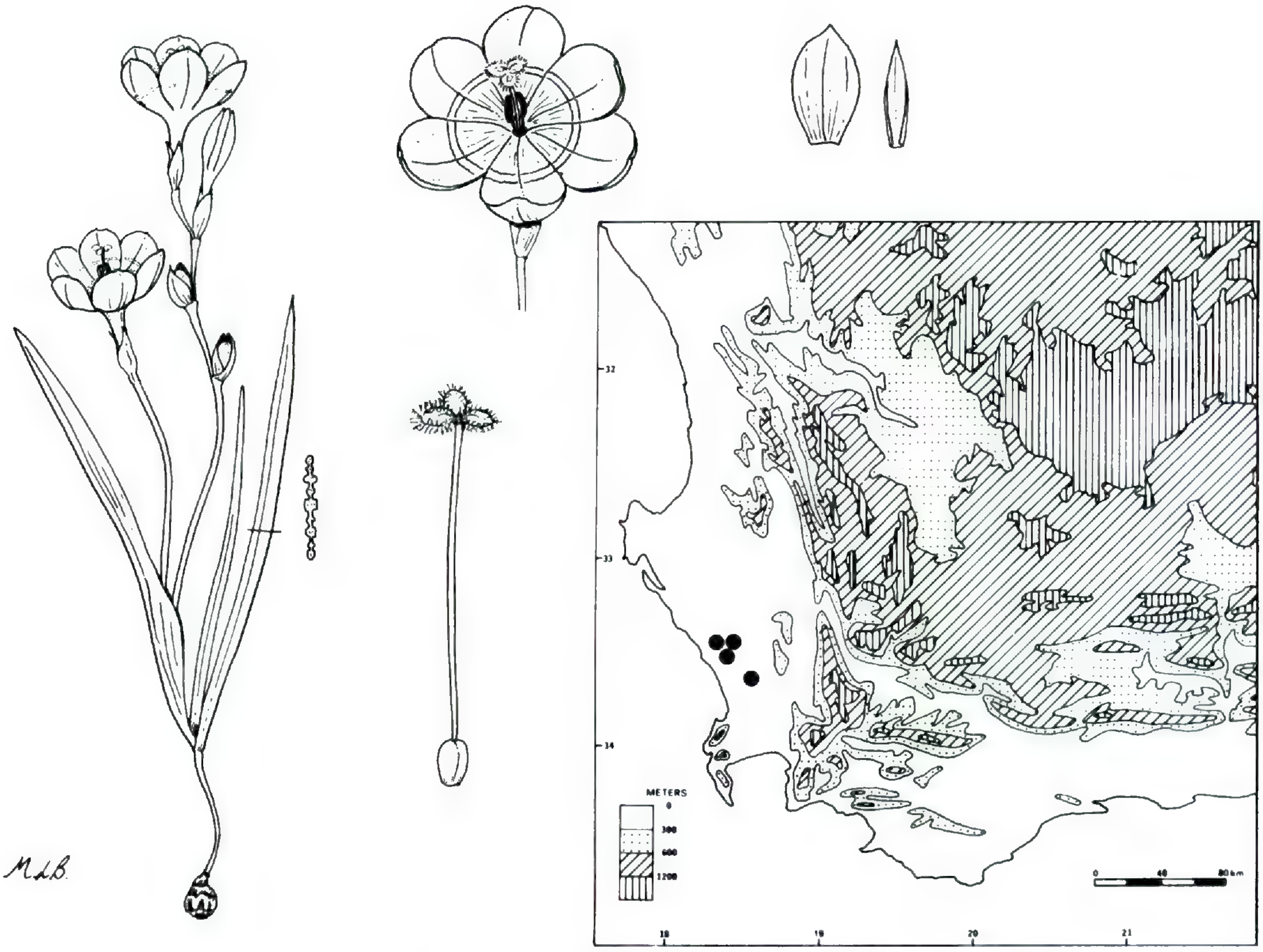


FIGURE 64. Morphology and distribution of *Geissorhiza eurystigma*. Habit ×0.5; flower and separated bracts life size; gynoecium and leaf section much enlarged (*Burns s.n.*, farm Dassenberg, Kanonkop).

aments to 9 mm long, erect, equal; *anthers* 4.5–5.5 mm long, yellow. *Ovary* 2–3 mm long, *style* dividing near the apex of the anthers, branches 4 mm long, broad and heavily ciliate-pubescent. *Capsule* ovate-oblong, about as long as the bracts. *Chromosome number,* unknown.

Flowering time. September to early October.

Distribution. Western Cape coastal belt, centered around Darling and Mamre, and extending southeast to Kalabaskraal. Figure 64.

Geissorhiza eurystigma was first described in 1766 by Daniel de la Roche, who named it *Ixia secunda*. The type, in the Leiden Herbarium, is today still well enough preserved to make this identification certain (Goldblatt & Barnard, 1970). A year after the publication of *I. secunda,* Bergius (1767) described a second species (now *G. aspera* Goldbl.) also calling it *I. secunda,* and in the appendix to this work he cited de la Roche's *I. secunda*. While Bergius' species is today not considered a validly published species, but merely a misapplied name, the eighteenth century botanical community either ignored the priority of de la Roche's species, or considered it and the better known Bergius plant conspecific (e.g., Thunberg, 1783), and the name was used widely for the small blue-flowered *G. aspera*.

Ker (1802a, 1802b) realized that *Ixia secunda* de la Roche was different from the species then bearing this epithet, but instead of applying the name *I. secunda* to what he believed was de la Roche's species, he renamed it *I. rochensis* and continued to use *I. secunda* in Bergius' sense. Ker included two species in *I. rochensis*, the filiform leaved plant figured in the "Botanical Magazine," now *G. radians* (long known as *G. rochensis*) and a variety (B) *spithamaea,* which in fact corresponds with de la Roche's *I. secunda,* now *G. eurystigma*. The two species are similar in flower form and color but *G. eurystigma* has broader, multi-ribbed leaves, broad flat ciliate

style branches and tepals which lack the white band and curious pits in the tepals characteristic of *G. radians*.

Robert Sweet realized that Ker's *Geissorhiza rochensis*, as figured in the "Botanical Magazine," was distinct from *Ixia secunda* de la Roche and in 1830 he renamed the latter *G. monantha*, citing a figure published by Houttuyn (1780) which is correctly named *I. secunda* de la Roche. In his catalogue of plants cultivated in Britain, Sweet (1830) also recognized Ker's *G. rochensis* (i.e., *G. radians*) as *G. rocheana*, indicating that he regarded the two as separate species. The name *G. monantha* is here considered a homonym of *G. monanthos* Ecklon. The two names have slightly different endings, one Greek and the other Latin, but they are certain to be confused and should not both be used in the same genus.

When *Geissorhiza eurystigma* was collected in the 1820s by Zeyher and then in the later nineteenth century by Templeman, it was again confused with the more common *G. radians* (*G. rochensis* sensu auct.) and robust plants of both species were referred to *G. rochensis* var. *spithamaea* Ker. Then in 1931 Louisa Bolus recollected the species and, believing that it was new to science, described it as *G. eurystigma*, a name referring to its unusual and conspicuous style branches. Foster (1941) regarded *Geissorhiza eurystigma* as a variety of the related *G. mathewsii*, a treatment not followed here. The differences between the two seem to me sufficiently great to merit separation at the species level, even though they share so unusual a character as their broad flat style branches. The two species are almost certainly closely allied. Both have relatively broad, ribbed leaves, deep blue flowers with a red center, and conspicuous broad flat style branches. The differences between the two species are discussed under *G. mathewsii*, the following species.

Specimens examined. SOUTH AFRICA. CAPE: 3318 (Cape Town), Mamre Hills (AD), *Barker 1810* (BOL, NBG), *3834* (NBG), *Wasserfall 436* (NBG), *van Niekerk 272* (NBG), *Compton 11765* (NBG); near Mamre (AD-CB), *L. Bolus s.n.* (BOL 19876), *Sidey 2283* (S); Groene Kloof, *Zeyher 295* in part (SAM 22086), *Templeman sub MacOwan 2281* (M, SAM, Z); 4 mi. N of Mamre on Darling road, *Lewis 1037* (SAM); between Mamre and Darling, *Lewis 3634* (SAM), *Lamb s.n.* (K), *Gillett 2074* (K); between Mamre and Darling at the turnoff to Mud River, *Goldblatt 7266* (MO); first gate to Ganzekraal (CB), *Barker 723* (NBG); Kalabaskraal (DA), *Werdermann & Oberdieck 323* (B, GH, K, PRE), *Strey s.n.* (M); farm Dassenberg, N slopes of Kanonkop Range, *Burns s.n.* (MO).

WITHOUT PRECISE LOCALITY: Cape, *Anon. s.n.* "*Ixia secunda* de la Roche" (L), Herb. Burman *s.n.* "*Gladiolus junceus*" (G), *Masson s.n.* (BM).

58. Geissorhiza mathewsii L. Bolus, Ann. Bolus Herb. 4: 42. 1926; Foster, Contr. Gray Herb. 135: 27. 1941, excluding var. *eurystigma*. TYPE: South Africa. Cape: damp marshy places near Darling, *Mathews s.n.* flor. 1923 (lectotype, BOL 18502, here designated); *Mathews s.n.* flor. 1926 (syntype, BOL 18502). FIGURES 10, 65.

Plants 8–18 cm high. *Corm* globose, more or less symmetric, 7–10 mm diam., truncate at base, tunics imbricate, blackish, layers notched below into regular segments. *Cataphyll* membranous or evidently lacking. *Leaves* 3, the lower two basal, reaching to base or middle of spike, 2–4 mm wide, ensiform, conspicuously several ribbed, lowermost smallest, the third and uppermost leaf inserted at base or in lower part of stem, sheathing and inflated below, also several ribbed, longer and larger than lower leaves. *Stem* flexed above sheath of upper leaf, and at base of inflorescence, smooth, rarely bearing a bract-like leaf in upper half, simple or 1–3-branched. *Spike* secund, flexuose, 2–6-flowered; *bracts* herbaceous, green, becoming dry and membranous from apex, and often reddish on upper margin, 6–12(–15) mm long, inner about as long but narrow. *Flowers* actinomorphic, nearly stellate when fully open, deep blue, with a red center sometimes outlined in white; *perianth tube* short and slender, 2–3 mm long, included in the bracts; *tepals* 14–16 mm long, 9–10 mm wide, obovate, blue above, reddish in lower half. *Filaments* 6.5–8 mm long, erect; *anthers* ca. 4.5 mm long, articulated and horizontal, lying over the style branches, brown-purple. *Ovary* ca. 2 mm long; *style* dividing near the base of the anthers, branches 2–3.5 mm long, broad and flat, evidently smooth, concealed by the anthers. *Capsule* globose, to 16 mm long. *Chromosome number*, unknown.

Flowering time. Mid- to late September.

Distribution. The Darling area of the west coast in wet low lying situations. Figure 65.

Geissorhiza mathewsii is a rare local endemic of the Darling area of the southwestern Cape coast where it grows in wet, low lying areas. It is related to and often confused with *G. eurystigma*. The two have a similar appearance and broad, ribbed leaves, blue flowers with a red center, and the peculiar broad flat style branches,

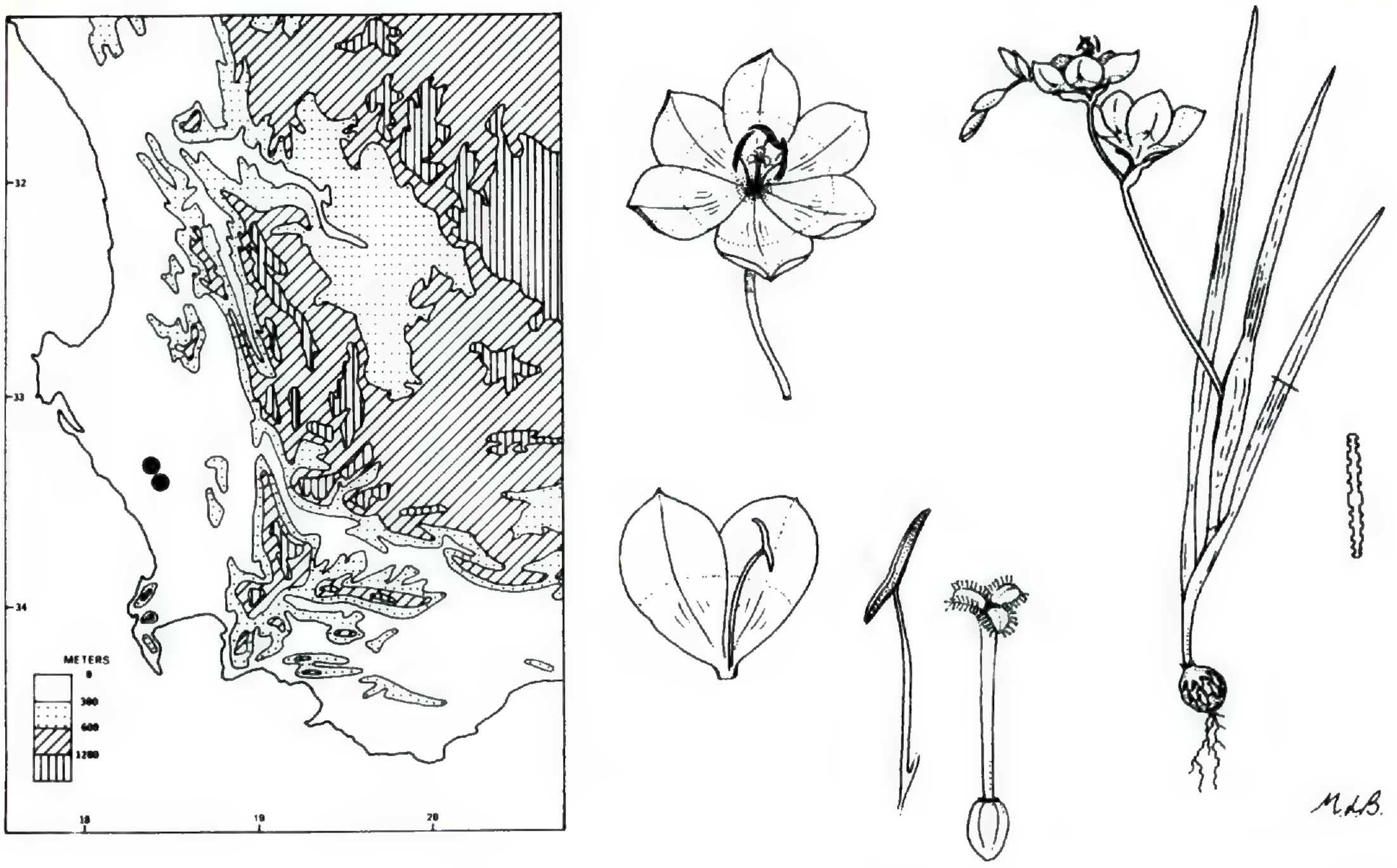


FIGURE 65. Morphology and distribution of *Geissorhiza mathewsii*. Habit ×0.5; flower and separate tepals life size; gynoecium and anther ×2; leaf section much enlarged (*Goldblatt 7268*, Waylands, Darling).

unique to these two species. Foster (1941) treated *G. eurystigma* as a variety of *G. mathewsii*, remarking that it differed primarily in its longer perianth tube, shorter filaments, and longer style. In this distinction Foster is only partly correct, *G. mathewsii* has a short tube, to 2.5 mm long and a shorter style but its filaments are shorter than those of *G. eurystigma*. However, there are other differences between the two and their treatment as separate is desirable. In addition to the short perianth tube, *G. mathewsii* has an altogether smaller flower with tepals to 16 mm long, whereas the tepals of *G. eurystigma* are up to 24 mm long. More significantly, the stamens and style are quite different. In *G. eurystigma*, the stamens are erect and held below the broad and heavily ciliate style branches, but in *G. mathewsii* the style divides near the base of the anthers which are articulated and lie horizontally when the flower is fully open, covering the nearly smooth style branches. The floral bracts also tend to be shorter than those of *C. eurystigma* and the lowermost leaf smaller than the others. The species is known from relatively few collections and is apparently very restricted in its distribution.

The distinctive flower coloring of *Geissorhiza mathewsii* and *G. eurystigma* is also found in *G. radians* and in some forms of the unrelated *G. monanthos* (section *Planifolia*), and they may be sometimes be confused. *Geissorhiza radians* can be recognized by the pitted markings on the tepals, narrow leaves, and longer perianth tube and *G. monanthos* by its puberulous stem and smooth, flat leaves. Similarity of floral coloration in *G. monanthos* is most likely due to color mimicry, common in the southwestern Cape flora. *Geissorhiza mathewsii* grows together with *G. radians* and *G. monanthos* at some sites and the differences between their habitat preferences is then evident. *Geissorhiza radians* grows in the wettest places, often in standing water; *G. mathewsii* prefers slightly higher ground, but still in waterlogged soil; and *G. monanthos* occurs only in well-drained areas surrounding wet depressions.

Specimens examined. SOUTH AFRICA. CAPE: 3319 (Cape Town) "in humidis" near Darling (AD), *Mathews s.n.* (BOL 18502); near Darling, *Compton & Lamb s.n.* (Nat. Bot. Gard. 1332/31 in BOL); Oudepos, Darling, *Lewis 2236* (SAM); Mr. Basson's farm near Darling, *Barker 6764* (NBG); between Mamre and Darling, *Lamb s.n.* (K); Waylands farm, edge of vlei N of the railway line, *Goldblatt 7268* (K, MO, NBG, PRE), *Jarvis s.n.* (MO).

WITHOUT PRECISE LOCALITY: Malmesbury (? distr.), *Kassner s.n.* (B).

59. Geissorhiza radians (Thunb.) Goldbl., Nordic J. Bot. 3: 441. 1983. *Ixia radians* Thunb., Phytogr. Blätt. 1: 3. 1803. TYPE: South Africa. Cape: exact locality unknown, *Thunberg s.n.* [lectotype, Herb. Thunb. 982 UPS, designated by Goldblatt (1982); syntype, Herb. Thunb. 983 UPS = *Romulea* sp.]. FIGURES 11, 66.

Ixia rochensis Ker, Bot. Mag. 17: tab. 598. 1802, nom. illeg. superfl. pro *I. secunda* de la Roche (1766) = *Geissorhiza eurystigma* L. Bolus. *Geissorhiza rochensis* (Ker) Ker, Ann. Bot. (König & Sims) 1: 224. 1804, nom. illeg. basion. illeg. superfl.; Baker, Handb. Irid. 156. 1892, Fl. Cap. 6: 71. 1896 excl. var. *monantha*; Foster, Contr. Gray Herb. 135: 29. 1941.

Ixia larochei Roemer & Schultes, Syst. Veg. 1: 379. 1817, nom. superfl. pro *I. secunda* de la Roche = *G. eurystigma* L. Bolus. *Geissorhiza larochei* (Roem. & Schult.) Loudon, Hort. Brit. 1st edition, 16. 1830, nom. illeg. basion. illeg. superfl.

Geissorhiza rocheana Sweet, Hort. Brit. 1st edition, 399. 1827, Hort. Brit. 2nd edition, 503. 1830. TYPE: South Africa. Cape: without locality (illustration in Bot. Mag. 71: tab. 598. 1802).

Geissorhiza tulipifera Klatt, Abh. Naturf. Ges. Halle 15: 390 (Erg. 56) 1882. TYPE: South Africa. Cape: near Paarl, *Drège 8486* (holotype, B, "Herb. Lubeck"; isotypes, G, K, L, MO, P, S).

Geissorhiza cyanea Ecklon, Topogr. Verz. Pflanzensamml. Ecklon 20. 1827, nom. nud. et ms. (*Ecklon & Zeyher Irid. 219*).

Geissorhiza rochensis var. *spithamaea* (Ker) Baker, Handb. Irid. 156. 1892, Fl. Cap. 6: 71. 1896 as to most specimens cited but excl. basion.; Foster, Contr. Gray Herb. 135: 29–30. 1941, pro parte (the type of var. *spithamaea* is *G. eurystigma* L. Bolus).

Rochea venusta Salisb., Trans. Hort. Soc. London 1: 322. 1812, nom. nov. pro *Ixia rochensis* Ker sensu Ker, nom. illeg. gen. illeg. non val. descr.

"*Geissorhiza radians* Gawl.," Nom. Bot. 2nd edition, 1: 668. 1840, in syn.

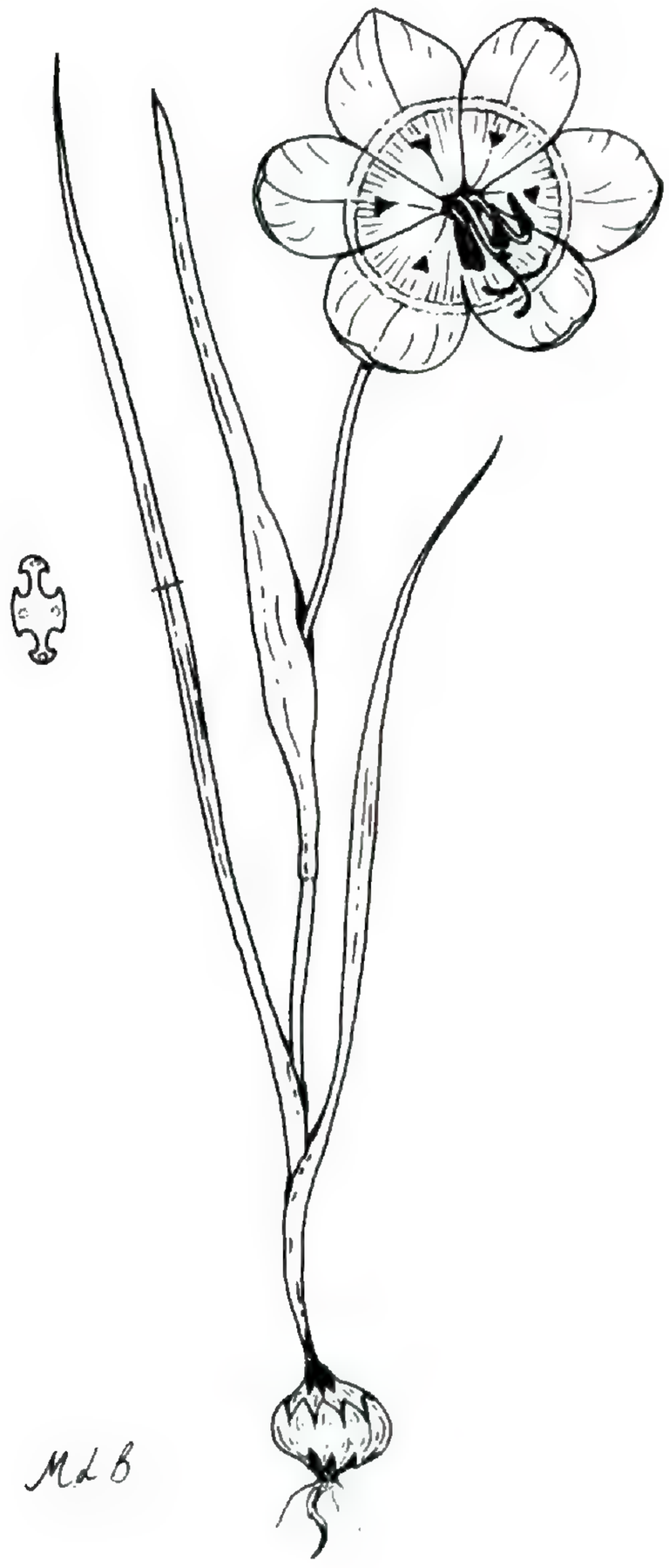
Plants 8–16 cm high. *Corm* globose, symmetric, truncate below, 6–9 mm diam., tunics dark, imbricate, notched below into regular rectangular segments. *Cataphyll* membranous pale. *Leaves* 3, linear, 0.5–1.5 mm wide, with thickened margins and enlarged midrib and 2-grooved on each surface, about as long, somewhat longer, or shorter than the stem, the lower two leaves basal, the upper inserted on lower part of stem, the sheath inflated and ribbed. *Stem* erect, flexed above the sheath of the upper leaf and at the base of the spike, simple or 1-branched. *Spike* 1–4 (–6)-flowered; *bracts* 8–13(–16) mm long, herbaceous, the inner shorter than the outer. *Flowers* zygomorphic with the stamens declinate, the tepals widely cupped, deep blue with a red center and narrow white band between, with a dark, excavated pit in the midline of each tepal; *perianth tube* 6–8 mm long, infundibuliform, exserted from the tube; *tepals* 15–22 mm long, obovate, 12–15 mm wide. *Filaments* ca. 10 mm long, equal, unilateral and declinate, held above the dorsal tepal, curving upward near the anthers; *anthers* unilateral, erect, 5–6 mm long, pollen red-brown. *Ovary* 2–3 mm long, *style* lying under the stamens, ca. 2 mm long, branches 4 mm, recurved. *Capsule* unknown. *Chromosome number,* unknown.

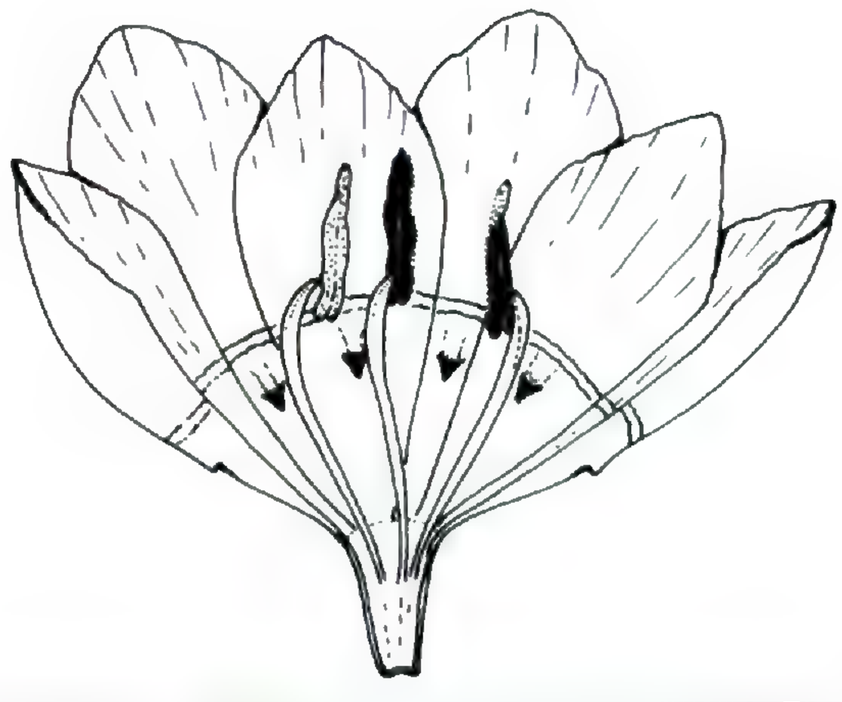
Flowering time. September to early October.

Distribution. Flats in the western Cape coastal belt, from the Darling area south to Paarl and possibly to False Bay, damp sites in sandy soil, often of granitic origin. Figure 66.

This species is one of the most striking in the genus, and one of few, fairly widely known. It is occasionally found in cultivation and its large, deep blue flowers with contrasting white band around the red center make it worth the effort to maintain the plant in garden situations. As is the case with many species that have received botanical attention over a long period, it has a complex nomenclatural history. It is also unfortunate that the name it has been known by for over 150 years, *Geissorhiza rochensis,* is illegitimate (Goldblatt, 1983), so that this well-known species now has to carry the new name *G. radians* (Thunb.) Goldbl.

The type collection of *Geissorhiza radians* was made by Thunberg in the 1770s, although he only described the species years later in 1803, as *Ixia radians.* A year before, Ker (1802a) published *Ixia rochensis* as a new name for *Ixia secunda* de la Roche, but based on plants grown in England, and figured in the "Botanical Magazine." Ker mistakenly believed the figured species to be the same as the *Ixia secunda,* described in 1766 by Daniel de la Roche, but this is actually conspecific with the superficially similar *G. eurystigma* L. Bolus. Ker used the name *Ixia secunda* for a third species, the small, blue-flowered *G. aspera,* and so cited *I. secunda* de la Roche as a synonym of his *I. rochensis.* Ker's nomenclatural treatment is unacceptable and today *I. rochensis* is regarded as a superfluous and illegitimate name (Goldblatt, 1983). The next available synonym for the species figured by Ker is *Ixia radians* Thunberg, and the combination in *Geissorhiza* was made in 1983 (Goldblatt, 1983).





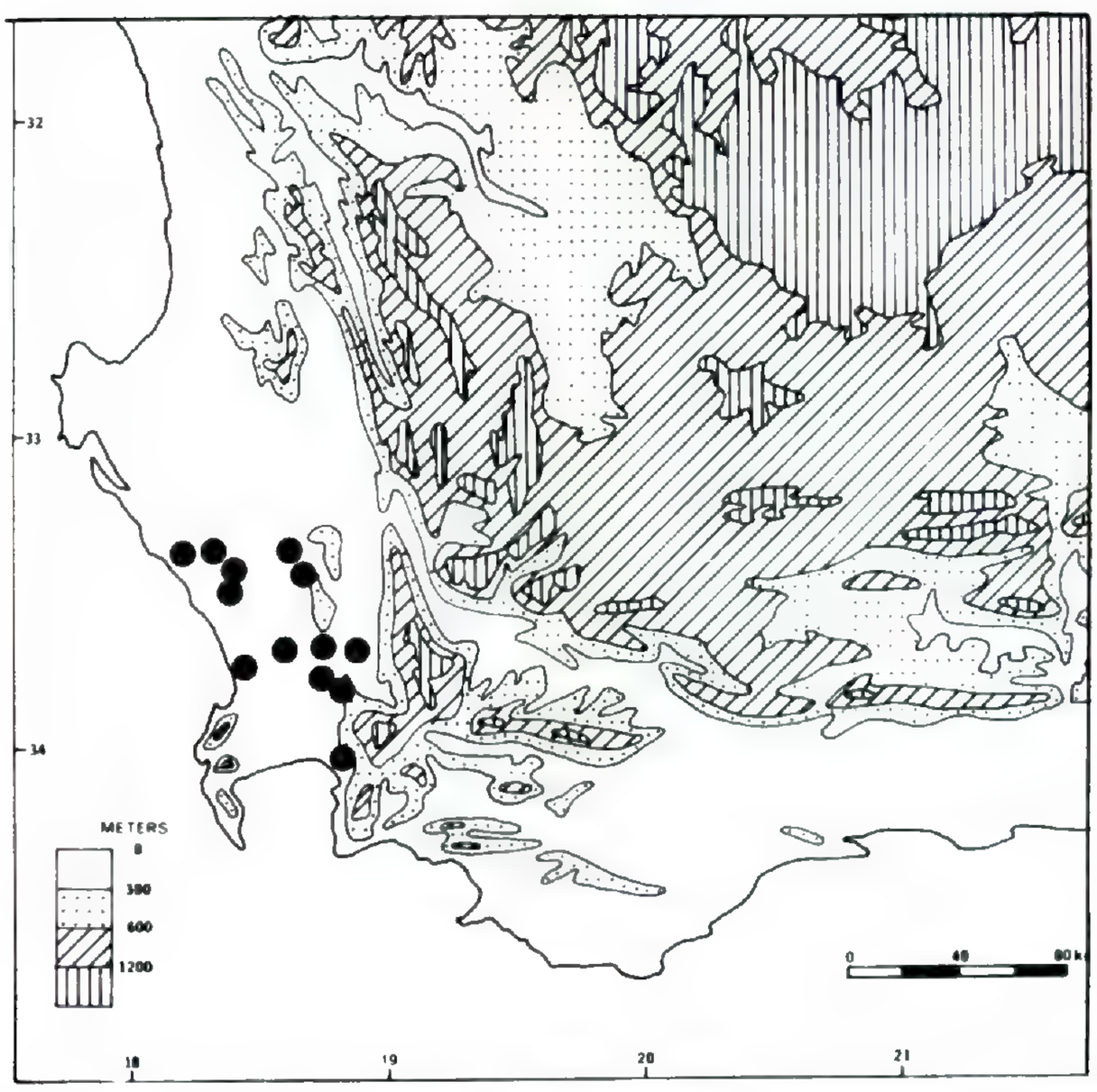


FIGURE 66. **Morphology and distribution of *Geissorhiza radians*.** Habit life size; opened flower ×1.5; leaf section much enlarged (cultivated plant, hort. Kirstenbosch, no voucher).

Sweet (1830) seems to have been aware of this confusion and he renamed *I. secunda* de la Roche, *G. monantha,* and *G. rochensis* sensu Ker, *G. rocheana.* Other synonyms of *G. radians* include *G. tulipifera* Klatt, merely a later synonym, and *G. cyanea* Ecklon, a nomen nudum. Robust specimens of *G. radians* have often been referred to *G. rochensis* var. *spithamaea* by both Baker (1896) and Foster (1941). There is no character other than size to distinguish the plants to which they applied the name and no infraspecific taxon of *G. radians* is recognized here. The type of var. *spithamaea* Ker, *Masson s.n.* "*Ixia violacea,*" in the British Museum is actually the closely related *G. eurystigma* (syn. *G. monantha* Sweet), which Ker regarded as a variety of his *G. rochensis.*

Geissorhiza radians was once fairly common along the Cape west coast, originally extending from False Bay in the south to the Malmesbury district in the north. Its range is now much reduced due to expanding farming activity. This is unfortunately inevitable, as *G. radians* grows along streams and in wet flats in a rich agricultural area. It is protected to some degree in small reserves in the Darling area by local farmers, at least from direct ploughing, but alien plant species, animal grazing, and effects of fertilizer and weed killer runoff are gradually changing the environment, and this and many other lowland west coast species are becoming increasingly threatened.

Geissorhiza radians is distinctive in its blue and red flower coloration and peculiar pitted markings in the midline of its tepals as well as in its linear (sometimes almost terete) leaves with enlarged margins and midrib. Similarly colored flowers are found in *G. mathewsii* and *G. eurystigma,* both of which lack the pitted tepal mark-

ings and have broad, ribbed leaves. Some forms of the unrelated *G. monanthos* also have similarly colored flowers but this species has flat leaves and a puberulent stem.

Specimens examined. SOUTH AFRICA. CAPE: 3318 (Cape Town) Ysterfontein (AC), *Barker 3844* (NBG); Groenekloof (AD), *Ecklon & Zeyher 219* (66) (B, FI, G, MO), *Zeyher 295* (SAM), *MacOwan s.n. in Herb. Norm. Austr. Afr. 506* (B, BM, BOL, G, GH, K, SAM, W, Z); near Groenekloof, *H. Bolus 4340* (BOL, K), *Pappe s.n.* (BM, K); near Darling, *H. Bolus 12843* (BM, BOL, BR, Z), *Levyns 3248* (K); Darling, *Guthrie 2054* (NBG), *Stokoe s.n.* (SAM 69599), *Grant 2527* (BOL, BR, M, MO, WAG), *Marloth 9562* (STE); Darling Flora Reserve, *Barker 8644* (NBG), *Lewis 5068* (NBG), *5537* (NBG); 8 mi. W of Darling, *Strey s.n.* (M); Mamre Hills, *Wasserfal 437* (NBG), *Barker 1806* (NBG), *3838* (NBG); between Mamre and Darling, *Lewis 3634* (SAM); 3 mi. S of Darling, *Lewis 1306* (SAM); streams near Malmesbury (BC), *Schlechter 1610* (B, G, W, Z); Melkbos-Strand road (CB-CD), Spenglersdrift, near Klipheuwel (DA), *Thompson 2597* (STE); Michiel Heyns, near Mamre Road, *Esterhuysen s.n.* (MO, PRE, S, US, WAG); 5.3 mi. NE of Klipheuwel Station, *Acocks 20645* (NBG, PRE); Agterpaarl, damp sites (DB), *Loubser 468* (NBG); near Paarl, *Drège 8486* (B, BM, G, K, L, MO, P, S); Muldersvlei (DD), *Lewis 4446* (SAM); damp place S of Bottelary road, *Acocks 2162* (S).

3418 (Simonstown) Hottentots Holland (BB), *Ecklon & Zeyher Irid. 292* (MO).

WITHOUT PRECISE LOCALITY: Herb. Burman *s.n.* "*Ixia secunda* Berg. Cap. 6" (G), *Oldenburg 59* (BM).

SECTION *MONTICOLA*

10. Section Monticola Goldbl., sect. nov. TYPE: *G. burchellii* Foster.

Tunicae cormi durae et lignosae vel molles, foliis plerumque 3, ensiformibus ad linearibus vel teretibus planis vel marginibus costisque incrassatis, caule glabro, bracteis herbaceis supra interdum siccis membranaceis, floribus actinomorphis stellatis vel declinatis, tubo brevi vel longo, staminibus aequalibus vel inaequalibus.

Corm tunics hard and woody to fairly soft in texture, *leaves* ensiform to linear or terete, more or less plane or with the margins and midrib variously thickened, *bracts* herbaceous below, becoming dry above, *flowers* stellate to hypocrateriform, actinomorphic or declinate, the tube short or reaching to the apex of the bracts, stamens equal or more often strongly unequal.

Species. 9.

60. Geissorhiza burchellii Foster, Contr. Gray Herb. 135: 25–26. 1941. TYPE: South Africa. Cape: Langeberg near Zuurbraak, *Schlechter 2160* (holotype, B; isotypes, B, BM, BOL, BR, PRE, Z). FIGURE 67.

Plants 12–20 cm high. *Corm* globose, tapering above, 7 mm diam., tunics light brown, more or less imbricate, papery in texture, cut below into narrow segments, drawn into points above. *Cataphyll* membranous, apparently solitary. *Leaves* 2–4, about half as long as the stem, occasionally about as long, 1.5–3 mm wide, the margins and midrib thickened and 2-grooved on each surface, often sticky and with soil adhering below, the lowermost leaf basal, the others inserted towards base and sheathing the stem for some distance above the ground, the uppermost sheathing for half its length. *Stem* erect, smooth, bearing in addition to a cauline leaf, 1–3 short, sheathing bracts, simple or 1–3-branched, flexed at the base of the inflorescence when in bud. *Spike* (1–)3–9-flowered, flexuose; *bracts* (6–)8–10 mm long, herbaceous, flushed red above. *Flower* stellate when fully open, the tepals sometimes becoming reflexed with age, pale to deep purple or violet, pale yellow in the throat and tube; *perianth tube* 4–6 mm long, cylindric, about as long or slightly longer than the bracts; *tepals* 12–18(–22) mm long, 5–6 mm wide. *Filaments* unequal, the two longer 10–14 mm long, the shorter 6–10 mm long; *anthers* yellow, 4–5.5 mm long. *Ovary* 1.5–2 mm long, *style* dividing near the apex of the anthers, branches ca. 4 mm long, recurved. *Capsule* more or less globose, 5–7 mm long. *Chromosome number*, $2n = 26$ (*Esterhuysen 35363*).

Flowering time. December to January.

Distribution. Mid to upper elevations in the Slanghoek, Hottentots Holland, Riviersonderend and Langeberg Mountains, between Bains Kloof and Heidelberg, blooming well only after fires. Figure 67.

Geissorhiza burchellii is an attractive but poorly known species of the western Cape mountains. It extends from the Slanghoek Mountains in the north to the Langeberg at Swellendam in the east and appears to grow at middle elevations on moist, often south-facing slopes. It flowers in the wild only after veld fires and in this character seems typical not only of the group of species to which it is allied but to most Cape mountain species of *Geissorhiza*.

It is related to *Geissorhiza grandiflora*, a species with a similar montane distribution and to the Cape Peninsula endemic *G. tabularis*, and is eas-

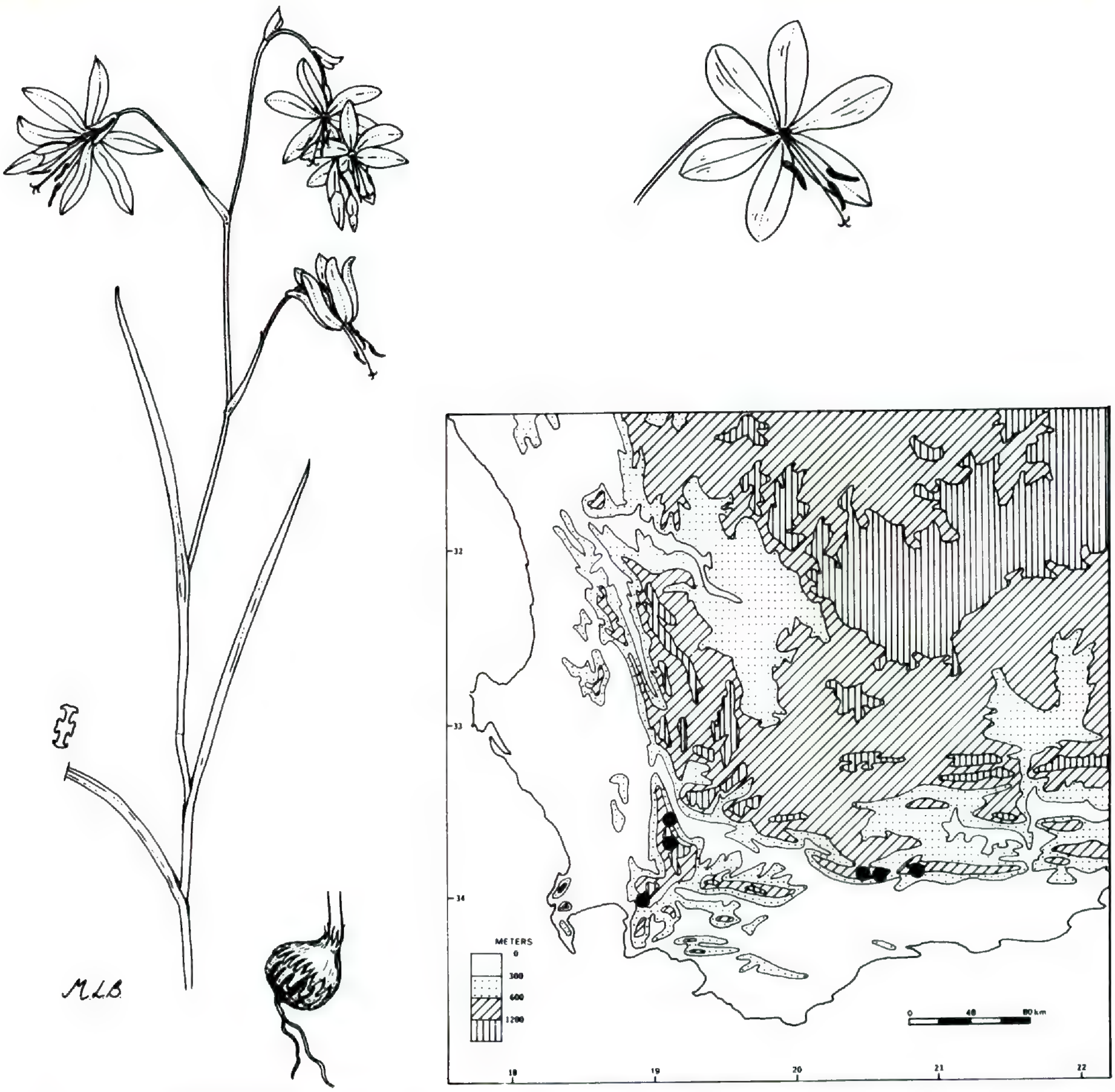


FIGURE 67. Morphology and distribution of *Geissorhiza burchellii*. Habit ×0.5; flower and corms life size; leaf section enlarged (*Esterhuysen 35159*, Goedehoop Peak, Langeberg).

ily confused with these species as well as with the more widespread *G. ramosa*. All are montane species with characteristic branched stems; papery to woody, more or less imbricate corm tunics; leaves with slightly to heavily raised margins and midrib; and distinctly unequal stamens. *Geissorhiza ramosa* stands out in having very small flowers with a perianth tube 2–3 mm long, tepals 5–9 mm long and anthers 2–3.5 mm long. The flowers of *G. tabularis* have a similar short tube 1.5–2 mm long, but are larger, with tepals 15–18 mm long and anthers 3.5–5 mm long. The flowers of *G. grandiflora* are even larger with a tube 10–22 mm long, tepals 22–30 mm long and anthers 5–6 mm long. *Geissorhiza burchellii* has flowers of intermediate size with a tube about 4–6 mm long, tepals 12–22 mm long and anthers 4–5.5 mm long. Its purple flowers and moderately long perianth tube give *G. burchellii* a very different appearance from the pale-flowered *G. tabularis* but it is easily confused with *G. grandiflora* and care must be taken in separating these two species.

A collection from Grassy Dome, Du Toits Kloof, *Jackson s.n.*, is tentatively assigned here. The single specimen lacks leaves and corm, but the flowers match those of *G. burchellii* well. Notes with sheet indicate that the flowers had white and dark red markings at the base of the tepals. Collections assigned here to *G. burchellii*

from near Caledon, *H. Bolus 9891,* and Landdrost Kop, *Stokoe s.n.* and *Thorne s.n.,* consist of plants within which the thickenings on the margins and midrib are poorly developed. In leaf morphology, these plants thus approach *G. grandiflora* but perianth tube and tepal length are nearly typical of *G. burchellii* and this is where they probably belong.

Specimens examined. SOUTH AFRICA. CAPE: 3318 (Cape Town) Landdrost Kop (BB), *Stokoe s.n.* (SAM 55712); E slopes of Landdrost Kop, *Thorne s.n.* (SAM 51559).

3319 (Worcester) Cossacks, Slanghoek Mts., 4,000 ft. (CA), *Esterhuysen 24006* (BOL, K, PRE); Grassy Dome, Du Toits Kloof, *Jackson s.n.* (NBG 88252).

3320 (Montagu) Twelve O'Clock Peak, above Swellendam, below summit, 4,800 ft., after fire (CD), *Esterhuysen 35363* (BOL, K, M, MO, NBG, P, PRE, S, US, WAG); Crown Mt., Swellendam, 3,800 ft., *Wurts 542* (NBG); Boskloof hut, Swellendam hiking trail, 3,000 ft., after burning, *Esterhuysen 35604* (K, MO, NBG, PRE, S, US, WAG); Langeberg near Zuurbraak, 3,300 ft. (DC), *Schlechter 2160* (B, BM, BOL, BR, PRE, Z); Goedehoop Peak, Heidelberg, steep moist S slopes in burned area, 3,500–4,000 ft. (DD), *Esterhuysen 35159* (BOL, K, MO, PRE, S, US); Langeberg above Grootvadersbos, 3,500–4,000 ft., *Esterhuysen 18273* (BOL, K, NBG, PRE).

WITHOUT PRECISE LOCALITY: hills near Caledon, *H. Bolus 9891* (BOL, K), *Burchell 7322* (K).

61. Geissorhiza grandiflora Goldbl., sp. nov. TYPE: South Africa. Cape: N side of Limietberg, Bains Kloof, ca. 4,000 ft., *Esterhuysen 35832* (holotype, BOL; isotypes, C, E, K, MO, NBG, PRE, S, US, WAG). FIGURE 68.

Planta 16–35 cm alta, foliis (2–)3 inferioribus duobus basalibus linearibus, marginibus costisque incrassatis, caule erecto saepe ramoso, spica (1–)3–8 florum, floribus hypocrateriformibus roseis, tubo perianthii (10–)15–22 mm longo, tepalis 22–30 mm longis, filamentis inaequalibus declinatis 11–20 mm longis, uno 4–5 mm breviore quam aliis, antheris 5–6 mm longis.

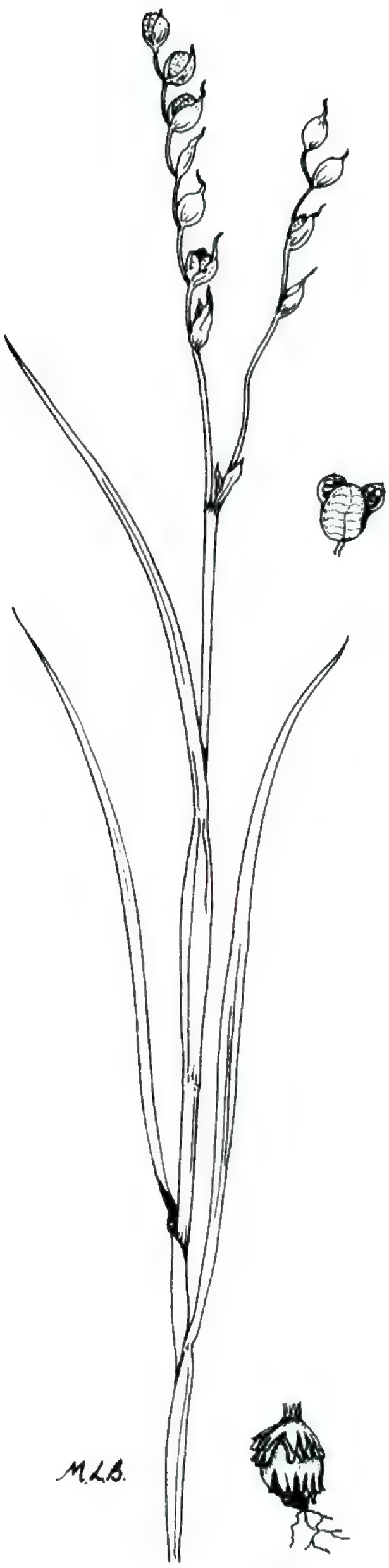
Plants 16–35 cm high. *Corm* globose, 10–12 mm diam., tunics brown, more or less imbricate, woody, cut below into segments and drawn into short points above. *Cataphyll* membranous, apparently solitary. *Leaves* (2–)3, linear, 1.5–4 mm wide, with thickened margins and midrib, 2-grooved on each surface, sometimes sticky below and with soil adhering, the lower one to two leaves basal, reaching to about the base of the spike, the uppermost inserted on the lower part of the stem and sheathing for some distance. *Stem* erect, smooth, bearing in addition to the cauline leaf, 1 or 2 short sheathing bracts, simple or 1–3-branched, flexed at the base of the spike in bud. *Spike* (1–)3–8-flowered, flexuose; *bracts* 13–16 mm long, herbaceous, flushed red above. *Flower* zygomorphic, the stamens and style declinate, deep pink with dark markings at the base of the tepals, pale in the tube; *perianth tube* (10–)15–22 mm long, cylindric, slightly longer to about twice as long as the bracts; *tepals* 22–30 mm long, 6.5–9 mm wide. *Filaments* unequal, unilateral and declinate, two 11–20 mm long, one 4–5 mm shorter than the others; *anthers* yellow, 5–6 mm long. *Ovary* 2–3 mm long, *style* dividing near the apex of the anthers, the branches 4–5 mm long, recurved. *Capsule* obovoid to globose, 5–8 mm long, enclosed in the bracts. *Chromosome number, 2n = 26 (Goldblatt 6828).*

Flowering time. Late November to early January.

Distribution. Mid to upper elevations in the Slanghoek, Hottentots Holland, Riviersonderend and Langeberg Mountains, in rocky habitats. Figure 68.

Geissorhiza grandiflora is endemic to the mountains of the southwestern Cape. It has been collected on isolated high areas from Great Winterhoek Mountain and Bains Kloof in the north to the Langeberg at Swellendam in the east. The relatively few collections suggest that it flowers irregularly, perhaps only after mountain fires. It has one of the largest flowers in the genus, comparable in size with those of some species of section *Engysiphon* (subgenus *Weihea*). Despite its large and zygomorphic flowers with declinate stamens and style, unusual in section *Monticola, G. grandiflora* has the imbricate corm tunics, unequal stamens and branched stems characteristic of this section and is assigned here rather than to section *Engysiphon.* It resembles most closely the smaller flowered *G. burchellii,* a generally smaller species that can be distinguished by its leaves with heavily thickened margins and midrib and actinomorphic flowers with tepals in the 12–18(–22) mm range and a perianth tube 4–6 mm long. *Geissorhiza burchellii* is most common in the Langeberg, but has been recorded to the west in the Hottentots Holland and Slanghoek Mountains as well. The two species are occasionally sympatric or nearly so and both have been collected on the Cossacks, Slanghoek Mountains, by Elsie Esterhuysen at the same time some years ago.

A collection from Great Winterhoek, *Phillips 1886,* is tentatively assigned to *Geissorhiza grandiflora.* It appears to have somewhat smaller



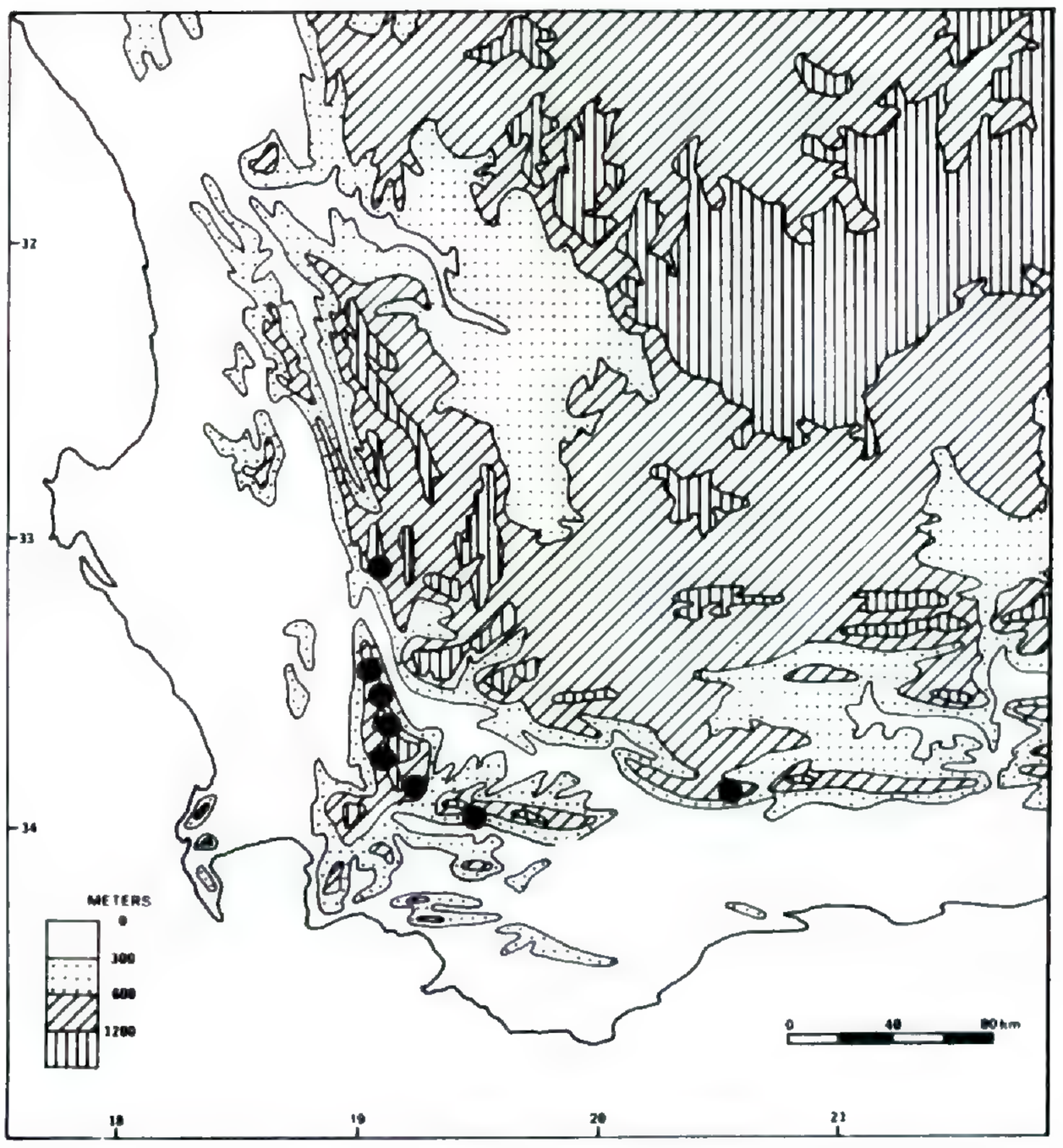


FIGURE 68. Morphology and distribution of *Geissorhiza grandiflora*. Fruiting plant and corm ×0.5; spike with flower and enlarged capsule life size (fruiting *Goldblatt 6828*, flowering *Esterhuysen 35832*, both Limietberg, Bains Kloof).

flowers than are typical, but it is uncertain whether the poorly pressed blooms were incompletely open or shrunk excessively on drying, or whether this represents a form that normally has flowers with shorter tepals. Also included are collections from the Riviersonderend Mountains, *Esterhuysen 35131*, and the Langeberg, *Wurts 543*. These comprise plants with somewhat atypical flowers, seemingly larger and with a wider perianth tube. The Esterhuysen collection clearly has yellow coloring in the throat of the flower. More collections from here are needed to determine whether this form represents a separate species.

Specimens examined. SOUTH AFRICA. CAPE: 3319 (Worcester) Great Winterhoek, ca. 5,000 ft. (AA), *Phillips 1886* (SAM); Cossacks, Slanghoek Mts., 4,000 ft. (CA), *Esterhuysen 23997* (BOL, K, MO, NBG); top of Baviaans Kloof off Bains Kloof, 3,000 ft., *Lewis 770*

or *s.n.* (BOL, NBG, PRE, SAM); N side of Limietberg, at the base and on a rocky slope, after a fire, *Esterhuysen 35832* (BOL, C, E, K, MO, NBG, PRE, S, US, WAG), *Goldblatt 6828* (MO, NBG, PRE); Haalsneeuwkop, 4,000 ft. (CC), *Stokoe s.n.* (SAM 56192); Wemmershoek Tafelberg, rugged slope, 5,000 ft., *Esterhuysen 35863A* (MO).

3320 (Montagu) Crown Mt., above Swellendam, 3,900 ft. (CD), *Wurts 543* (NBG).

3419 (Caledon) Villiersdorp, near the new power station (AA), *Herre s.n.* (STE 8984); Kanonkop, E side of Genadendal valley, low wet cliffs, ca. 3,000 ft. (BA), *Esterhuysen 35131* (BOL).

62. Geissorhiza tabularis Goldbl., sp. nov. TYPE: South Africa. Cape: Table Mt., between Skeleton and Window Gorges, *Goldblatt 6726* (holotype, MO; isotypes, K, NBG, PRE, S, US, WAG). FIGURE 69.

Geissorhiza ramosa (Ker) Klatt sensu G. J. Lewis, Fl. Cape Penins. 255. 1950.

Planta 25–35 cm alta, foliis (2–)3 inferioribus duobus basalibus linearibus marginibus costoque incrassatis, caule erecto, spica 3–8 florum, floribus stellatis malvinis, tubo perianthii ca. 1.5 mm longo, tepalis 15–18 mm longis, filamentis inaequalibus, longioribus duobus 5–6 mm longis, breviore 3–4 mm longo, antheris 3.5–5 mm longis.

Plants 25–35 cm high. *Corm* globose, tapering above, 7 mm diam., tunics light brown, more or less imbricate, papery in texture, cut below into narrow segments and drawn into points above. *Cataphyll* membranous, apparently solitary. *Leaves* (2–)3, linear, 2–3 mm wide, with slightly thickened to winged margins and midrib, and broadly 2-grooved on each surface, somewhat sticky below and with soil adhering, half to occasionally about as long as the stem, the lower two (or one) basal, the uppermost cauline, sheathing for half its length. *Stem* erect, smooth, bearing in addition to a cauline leaf, 1(–2) short, sheathing bracts, simple or 1–3-branched, flexed at the base of the inflorescence when in bud, later becoming straight. *Spike* 3–8-flowered, flexuose; *bracts* 7–8 mm long, herbaceous, flushed red above, recurved above at flowering time. *Flower* stellate when fully open, pale mauve to nearly white, usually becoming white after drying; *perianth tube* 1.5–2 mm long, cylindric, much shorter than the bracts; *tepals* 15–18 mm long, 5–7 mm wide. *Filaments* unequal, the two longer 5–6 mm long, the shorter 3–4 mm long; *anthers* 3.5–5 mm long. *Ovary* 1.5–2.5 mm long, *style* dividing at the apex of the anthers, branches ca. 2.5 mm, recurved. *Capsule* unknown. *Chromosome number*, $2n = 26$ (*Goldblatt 6726*).

Flowering time. Late October to mid-December.

Distribution. Restricted to the lower plateau of Table Mountain, in very wet or marshy situations in peaty sand, blooming rarely (if at all) except after fire. Figure 69.

This species, collected at least as early as 1825 by Ecklon and Zeyher, has long been confused with *Geissorhiza ramosa* Ker ex Klatt and it was so treated in "Flora of the Cape Peninsula" by Lewis (1950). Neither Foster (1941) nor Baker (1896) dealt with *Geissorhiza tabularis* and probably had no material of the species. It is endemic to Table Mountain on the Cape Peninsula and grows in wet or marshy sites. It flowers in the late spring or early summer only in the years following a veld fire.

Geissorhiza tabularis is related to the more common and widespread *G. ramosa* but is quite distinct from this species which typically has a more branched stem and many, much smaller flowers, the tepals of which are 5–9 mm long in contrast to the few branched *G. tabularis* in which the tepals range from 15–17 mm long. *Geissorhiza tabularis* seems close also to the widespread Cape mountain species, *G. burchellii,* which has large, purple flowers with a longer perianth tube to 5 mm and longer filaments, the long pair being 10–13 mm long and the short one, 5–8 mm. *Geissorhiza tabularis* has an unusually short perianth tube, 1.5–2 mm long and characteristically short filaments 3–6 mm long.

Specimens examined. SOUTH AFRICA. CAPE: 3318 (Cape Town) S slopes of Table Mt. (CD), *H. Bolus 3887* (BOL); Table Mt., top of Skeleton Gorge, burned last summer, *Esterhuysen 10579* (BOL, K), *Compton 16569* (BOL, NBG, STE, W); Table Mt. between Skeleton and Window Gorges, *Goldblatt 6726* (K, MO, NBG, PRE, S, US, WAG); Table Mt., lower plateau above Kirstenbosch, *Lewis 773* (PRE, SAM 56034); summit of Table Mt., *Zeyher s.n.* (SAM 20851); Groot Kop, shady S face, *Lewis 4792* (SAM), *Compton 19418* (BOL, NBG); Waai Vlei, *Wolley Dod 2146* (BM, BOL, K in part).

63. Geissorhiza ramosa Ker ex Klatt, Linnaea 34: 657. 1866 (perhaps intended as a combination but no basionym cited and thus regarded as a new species); Foster, Contr. Gray Herb. 135: 24. 1941. *Geissorhiza secunda* var. *ramosa* (Klatt) Baker, Handb. Irid. 155. 1892, Fl. Cap. 6: 69. 1896. TYPE: South Africa. Cape: Tulbaghskloof, Tulbaghsthal, am Fuss des Winterhoeksberg, am Witsenberg und bei Vogelvalei, *Ecklon &*

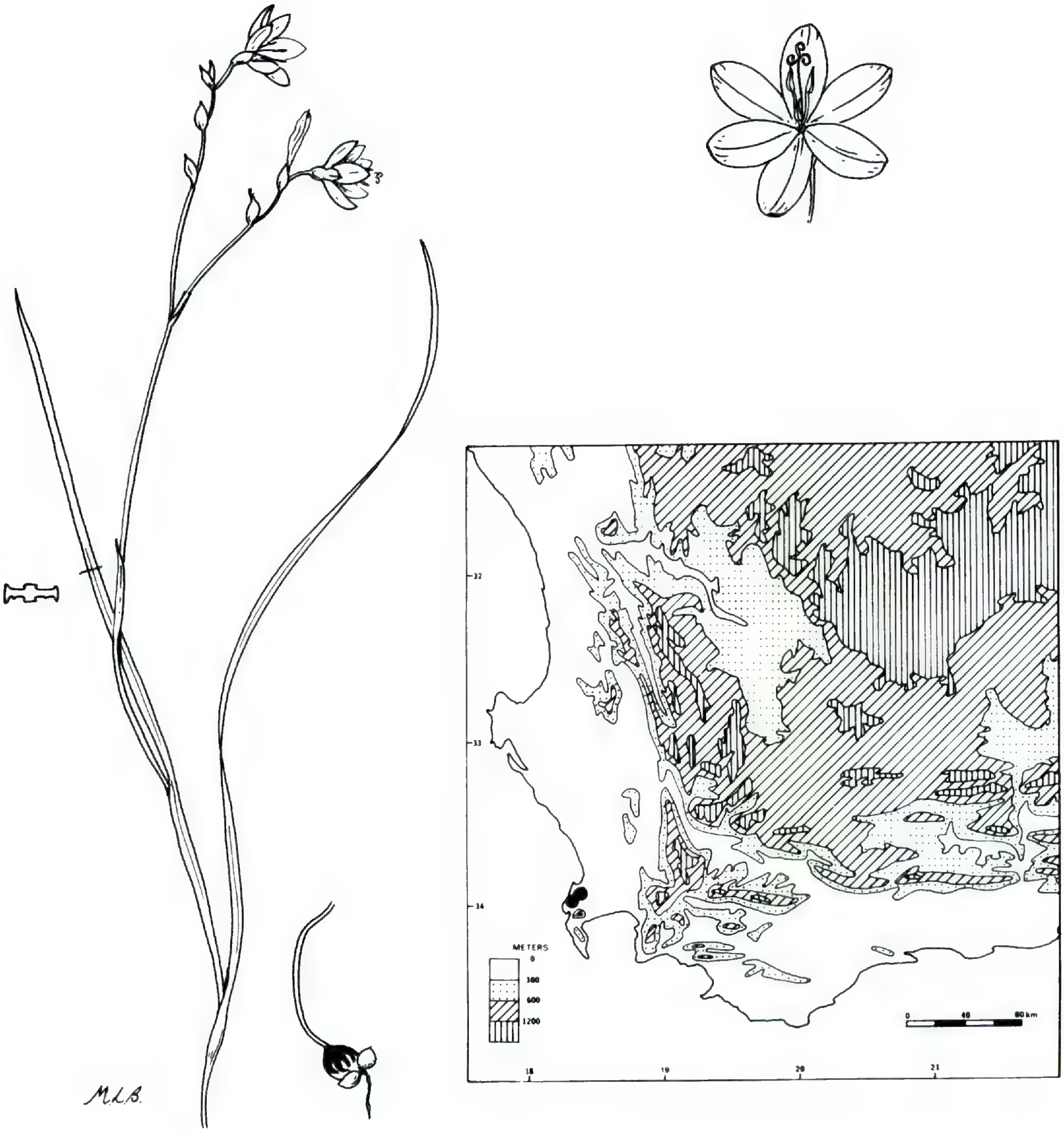


FIGURE 69. Morphology and distribution of *Geissorhiza tabularis*. Habit and corm ×0.5; flower life size (*Goldblatt 6726*, Table Mt.).

Zeyher Irid. 229 (77.11) [lectotype, B, designated by Foster (1941); isolectotypes, B, BM, E, FI, G, GH, L, LD, MO, P, PRE, SAM, W, Z], *Ecklon & Zeyher Irid. 234* (syntype, not seen).

Geissorhiza montana Foster, Contr. Gray Herb. 135: 55. 1941. TYPE: South Africa. Cape: Genadendal Mts. at 3,000–4,000 ft., *Drège s.n.* "*G. imbricata* α" (holotype, B; isotypes, BM, E, G, K, L, MO, S).

Plants 20–45 cm high. *Corm* globose, tapering above, 6–8 mm diam., tunics brown, woody or more often more or less papery in texture, incised below into regular sections. *Cataphyll* membranous, solitary. *Leaves* 2–3(–4), linear, 1–2.5 mm wide, the margins and midrib thickened and narrowly 2-grooved on each surface, half as long, to about as long as the stem, the lower one or two leaves basal, the upper one (rarely two) cauline, and sheathing the stem below. *Stem* erect, smooth, with 2–4 branches (rarely simple), usually bearing 1 cauline leaf and short bracts in the axils of the branches. *Spike* few to several (to 11)-flowered, inclined, flexuose; *bracts* (3–)4–5.5

mm long, herbaceous, or becoming dry and membranous from the apex. *Flower* evidently stellate and actinomorphic (not seen live), blue, purple, or violet (fading to pink then white when dry); *perianth tube* short, 2–3 mm long; *tepals* (5–)7–9 mm long, 3–4.5 mm wide, obovate. *Filaments* unequal, the two longer 3–4 mm long, the other shorter by 0.5–1.5 mm; *anthers* 2–3.5 mm long, yellow. *Ovary* 1–2 mm long, *style* dividing towards the apex of the anthers, branches ca. 1.5 mm long, recurved. *Capsule* globose to oblong, 3.5–5 mm long. *Chromosome number,* unknown.

Flowering time. October to December (to January at high elevations).

Distribution. Mountains of the southwestern Cape from Groot Winterhoek in the north to the Langeberg near Riversdale in the east, often in marshy or wet sites; frequent after fires. Figure 70.

Geissorhiza ramosa is relatively common in the mountains of the southwestern Cape but it is not often collected, probably because it grows mainly at high altitudes and also due to its habit of flowering well only after fires. It is a most distinctive species and its normally branched stem; small, short-tubed flowers, and unequal stamens make confusion with other species unlikely. It is most closely related to the Cape Peninsula endemic, *G. tabularis* a species with much larger flowers, but a shorter perianth tube. The relationships of *G. ramosa* are discussed more fully under this species.

Specimens collected at Vogelgat near Hermanus, *Schlechter 9577* and in Bains Kloof, *Grant s.n.,* are unusually short and have mostly unbranched stems and seem at first rather different from other collections of *G. ramosa.* The specimens match exactly the smaller individuals of collections such as *Esterhuysen 33703,* and there seems no reason to regard this material as anything but depauperate *G. ramosa.*

When Klatt described *Geissorhiza ramosa* he attributed the name to Ker, although as far as is known, Ker never knew this species. Klatt perhaps cited Ker in error or possibly intended to make a new combination based on *Ixia ramosa* Ker, but if so he neglected to cite a basionym, as was his normal practice. Given this situation, Foster (1941) suggested that *G. ramosa* be regarded as a new species described by Klatt, although he was aware that some 30 years later Klatt (1895) cited *Ixia ramosa* Ker in the synonymy of *G. ramosa* when he subsequently dealt with this species. Foster suggested that after this period of time this action could not serve to indicate that *G. ramosa* was originally a new combination. I propose to follow Foster's treatment of *G. ramosa.*

Foster also recognized *Geissorhiza montana,* here included in *G. ramosa.* He knew this only from the type collection, a population of small plants, which he considered distinct from *G. ramosa,* on account of its crowded basal leaves "with a different type of venation" and soft, imbricate corm tunics. In fact plants of the type collection, *Drège s.n.* "*G. imbricata* a," have only two basal leaves, as in all the specimens he placed in *G. ramosa,* with margin and midvein only slightly less thickened than in those of other specimens. The corm tunics differ, in my estimation, hardly at all from many other collections of typical *G. ramosa. Geissorhiza montana* is therefore reduced to synonymy in *G. ramosa.*

Specimens examined. SOUTH AFRICA. CAPE: 3318 (Cape Town) Jonkershoek (DD), *Compton 15310* (NBG).

3319 (Worcester) Winterhoeksberg (AA), *Ecklon & Zeyher Irid. 227* (72.11) (B, LD, P); Witsenberg, Tulbagh (AC), *Zeyher 1596* (B, FI, K, P, PRE, S, SAM, W, Z); Tulbagh ('Worcester, Tulbaghskloof'), *Ecklon & Zeyher Irid. 229* (77.11) (B, BM, E, FI, G, GH, L, LD, MO, PRE, S, SAM, W, Z); Tulbagh Waterfall, *Esterhuysen 16229* (BOL, NBG); mts. near Michells Pass (AD), *H. Bolus 5246* (BOL, K); Du Toits Kloof (CA), *Drège 8481a* (B, G, K, L, MO), *Lewis 3632* (MO, SAM), *Stokoe s.n.* (SAM 60127); suurvlakte, N of Du Toits Kloof, damp mossy bank, *Esterhuysen 12320* (BOL); Steenboksberg, Bains Kloof, marshy stream bank near "Veepos," *Esterhuysen 33703* (BOL, K, MO, S, US, WAG); Bains Kloof, *Grant s.n.* (LMU, MO, WAG); Witte River valley, Wellington, *Thorne s.n.* (SAM 46520), *Wasserfall 619* (NBG), *Esterhuysen 9430* (BOL); farm Eendracht, Waaihoek (CB), *Pica Survey s.n.* (PRE); mt. slopes S of Wemmershoek, 2,000 ft. (CC), *Phillips 1309* (SAM); Adolph's Kop, French Hoek Mts., *Esterhuysen 11198* (BOL, PRE); ridge from French Hoek Pass towards Paarde Kop, *Esterhuysen 35862* (MO); Zachariashoek, Kalsteelkloof, *Smith 46* (STE); Villiersdorp (CD), *Esterhuysen s.n.* (BOL 31883).

3320 (Montagu) forest path, below 10 O'Clock Mt., Swellendam (CD), *Wurts 455* (NBG); Swellendam Mt., 2,500 ft., *Galpin 4680* (K, PRE); Swellendam, above the town, 2,000 ft., *Taylor 4228* (STE); Tradouw Pass (DC), *Barnard s.n.* (SAM 28495), *Galpin 4679* (PRE).

3321 (Ladismith) Corente River farm, Riversdale (CC), *Muir 5364* (PRE); 'Valley River, on the Lange Bergen near Kampscheberg, Riversdale Division,' *Burchell 7044* (K).

3418 (Simonstown) Somerset Sneeukop (BB), *Stokoe s.n.* (SAM 49610); E slopes of Landrost Kop, Hot-

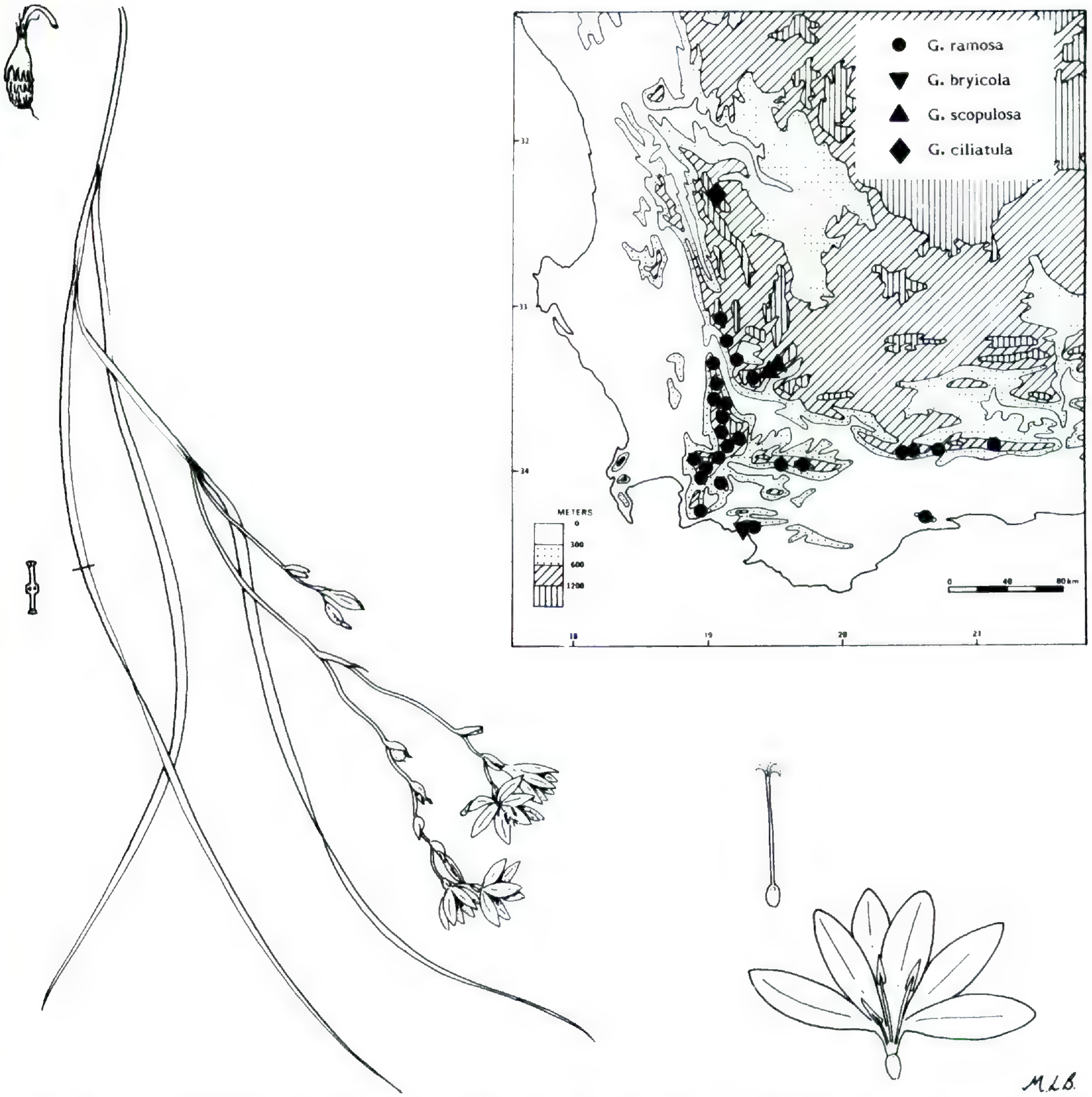


FIGURE 70. Morphology of *Geissorhiza bryicola* and distribution of *G. ramosa, G. bryicola, G. scopulosa,* and *G. ciliata.* Habit ×0.5; flower and gynoecium ×1.5 (*Goldblatt 7032,* Vogelgat, Hermanus).

tentots Holland, *Thorne s.n.* (SAM 51545); slopes above Steenbras Siding, *Thorne s.n.* (SAM 50416); Leopard Gorge, Betty's Bay, forest edge (BD), *Boucher 1704* (STE).

3419 (Caledon) Lebanon, burned area, 3,000 ft., *Kruger 227* (PRE, STE); Vogelgat (AD), *Schlechter 9577* (B, BM, BR, E, G, K, L, MO, P, PH, PRE, Z), *Goldblatt 6741* (MO); mts. above Genadendal (BA), *Drège s.n.* (B, BM, E, G, K, MO, S); Rivier Zonder End Mts. (BA-BB), *Stokoe s.n.* (SAM 57329); Pilaarkop above Lindeshof, path below summit, 4,500 ft. (BB), *Esterhuysen 35709* (K, MO, NBG, PRE, S, US, WAG).

3420 (Bredasdorp) limestone hills, Potteberg, De Hoop (AD), *Burgers 1197b* (PRE).

WITHOUT PRECISE LOCALITY: Caledon, *Pappe s.n.* (K); C. B. S., *Roxburgh s.n.* (BM).

64. Geissorhiza bryicola Goldbl., sp. nov. TYPE: South Africa. Cape: Vogelgat Nature Reserve, Hermanus, along the path at Psoralea Drip, *Goldblatt 7032* (holotype, MO; isotypes, K, NBG, PRE, S, WAG). FIGURE 70.

Planta 15–30 cm alta, cormo subgloboso, 5–8 mm diam., tunicis duro-membranaceis infra incisis, foliis 3(–4), inferioribus duobus basalibus linearibus, caule reclinato interdum ramoso, spica 2–6 florum, bracteis herbaceis, 4–6(–8) mm longis, floribus stellatis albis, tubo ca. 2.5 mm longo, tepalis 8–10 mm longis, filamentis inaequalibus, longioribus 5–6 mm longis, breviore 3.5–5 mm longo, antheris ca. 3 mm longis.

Plants 15–30 cm high. *Corm* subglobose, symmetric, 5–8 mm diam., tunics brown, brittle-membranous, imbricate, incised below into regular segments. *Cataphyll* membranous. *Leaves* usually 3(–4), linear, weak and trailing, usually slightly longer than the stem, 1.5–4 mm wide, nearly flat, the midrib and margins lightly raised, the lower two leaves basal, the third inserted in the lower to mid part of the stem, partly sheathing, occasionally bract-like and with a short free apex, the fourth leaf if present, inserted in the upper part of the stem and short, more often reduced to a scale. *Stem* weak, inclined to trailing, simple or with 1 (occasionally 2) branches, bearing 1 short leaf and sometimes a second, often bract-like shorter leaf. *Spike* (2–)3–6(–10)-flowered, flexuose; *bracts* 4–6(–8) mm long, herbaceous, the upper margins transparent. *Flower* stellate, white; *perianth tube* short, ca. 2.5 mm long, usually just exserted from the bracts; *tepals* 8–10 mm long. *Filaments* unequal, the two longer 4–6 mm long, the shorter 3.5–5 mm long; *anthers* ca. 3 mm long, yellow. *Ovary* 2–2.5 mm long, *style* dividing at the apex of the anthers, branches ca. 1.5 mm long, recurved. *Capsule* globose, 3–5 mm long. *Chromosome number*, $2n = 26$ (*Goldblatt 6741*), 26 + B (*Goldblatt 6742*).

Flowering time. September to mid-November.

Distribution. Klein River Mountains, in the vicinity of Hermanus, wet situations, in shade or on damp cliffs near seeps or waterfalls. Figure 70.

Geissorhiza bryicola grows in much the same habitat as *G. cataractarum*, which occurs along the slopes of the mountains between Hermanus and Bettys Bay some 30 km to the west. The two are, however, unrelated, and are treated here as belonging to different subgenera. *Geissorhiza bryicola* has smaller and white flowers (tepals 8–10 mm long) on spikes of 3–6 (occasionally to 10) flowers; unequal stamens; persistent, brown, imbricate corm tunic layers; and leaves with a nearly flat lamina. In contrast, *G. cataractarum* has large bluish flowers with tepals 14–20 mm long; spikes of 1–5 flowers; equal stamens; evanescent, pale evidently concentric corm tunics; and leaves with much thickened margins and midrib. *Geissorhiza bryicola* is closely related to the widespread western Cape mountain species *G. ramosa* and the two have similar flowers with short unequal stamens. *Geissorhiza ramosa* is a more robust species, usually with erect 2–4-branched stems, spikes of up to 11 flowers and leaves with thickened margins and midrib. This combined with a purple to violet flower make it unlikely to be confused with the white-flowered *G. bryicola*.

Specimens examined. SOUTH AFRICA. CAPE: 3419 (Caledon) Fernkloof Nature Reserve, Hermanus, rock face in spray of waterfall, 200 m (AD), *Robertson 132* (K, MO, NBG, PRE); Vogelgat Nature Reserve, along the path to Main Falls, *Goldblatt 6742* (MO, NBG), *7037* (MO, PRE, S); Vogelgat, wet S-facing rocks at Psoralea Drip, *Goldblatt 7032* (K, MO, NBG, PRE, S, WAG).

WITHOUT PRECISE LOCALITY: Hermanus Mts., *Stokoe s.n.* (SAM 55711); Klein River Mts., *Stokoe s.n.* (SAM 63476).

65. Geissorhiza scopulosa Goldbl., sp. nov. TYPE: South Africa. Cape: Hex River Mts., Milner Ridge Peak, 4,000–5,000 ft. (AD), *Esterhuysen 9328* (holotype, BOL; isotypes, NBG, PRE).

Planta 6–15(–20) cm alta, foliis 3 inferioribus duobus basalibus linearibus, marginibus costoque incrassatis, caule erecto vel inclinato, spica 2–7 florum, floribus stellatis coeruleo-violaceis, tubo perianthii 2–3 mm longo, tepalis 8–9 mm longis, filamentis inaequalibus, longioribus duobus ca. 3 mm longis, breviore 2 mm longo, antheris 2–2.5 mm longis.

Plants (6–)8–15(–20) cm high. *Corm* globose, 8–10 mm diam., tunics brown, firm to soft-membranous, imbricate, regularly notched below. *Cataphyll* membranous, brownish above. *Leaves* 3, linear, 1–2 mm wide, the margins raised at right angles to the lamina, the midrib thickened, the lower two leaves basal, the lowermost longest, reaching at least to the base of the spike, sheath sticky and with sand adhering, second leaf sheathing the lower part of the stem for a short distance, the uppermost inserted in the upper part of the stem, short, sheathing for at least half its length, sometimes almost entirely. *Stem* upright or inclined, simple, minutely ciliate-papillose, bearing in addition to a cauline leaf, a sheathing bract in the upper third. *Spike* secund, flexuose, 2–5(–7)-flowered; *bracts* 3.5–5 mm long, green to membranous in bud, sometimes reddish above, becoming dry and pale in the upper part at flowering time. *Flower* stellate, pale violet blue, darkening in color with age, cream in the throat and tube; *perianth tube* 2–3 mm long, infundibuliform; *tepals* 8–9 mm long, ca. 3 mm wide, elliptic. *Filaments* unequal, the two longer ca. 3 mm long, the shorter 2 mm long; *anthers* 2–2.5 mm long, yellow. *Ovary* ca. 1 mm long,

style dividing near the apex of the anthers, branches ca. 1 mm long, recurved. *Capsule* globose, to 4 mm long, not exceeding bracts. *Chromosome number,* unknown.

Flowering time. November.

Distribution. Damp rocky sites, in cliffs and under boulders, usually south-facing, at high altitudes in the Hex River Mountains. Figure 70.

Geissorhiza scopulosa is very like *G. ramosa* in floral morphology and general appearance, although much reduced in size, and the two are almost certainly closely related. *Geissorhiza scopulosa* is restricted to the Hex River Mountains, an area where *G. ramosa* does not occur. It is apparently confined to rocky habitats at altitudes above 1,500 m. In addition to its smaller size, *Geissorhiza scopulosa* can be recognized by its unbranched stems, which are minutely ciliate, an unusual character in this section. Its reduced size and absence of branching make it seem likely that *G. scopulosa* is a local segregate of the very widespread *G. ramosa.*

Specimens examined. SOUTH AFRICA. CAPE: 3319 (Worcester) Hex River Mts., Milner Ridge peak, 4,000–5,000 ft. (AD), *Esterhuysen 9328* (BOL, NBG, PRE); Milner Ridge Peak, S-facing cliffs, 5,000–6,000 ft., *Esterhuysen 9333* (BOL, NBG); Baboon Peak, Hex River Mts., 4,800 ft., *Esterhuysen 33337* (BOL).

66. Geissorhiza ciliatula Goldbl., sp. nov. TYPE: South Africa. Cape: Cedarberg, Middelberg, 1,500 m, *Goldblatt 5144* (holotype, MO; isotypes, K, NBG, S).

Planta 6–12 cm alta, tunicis cormi imbricatis mollibus, foliis (2–)3, inferiore basali falcato, marginibus costoque incrassatis, secundo basali caulem vaginanti in parte dimidio, superiore supra terram inserto vaginanti infra vel omnino, caule erecto ciliato, spica 1–4 florum, floribus stellatis albis postea purpurascentibus, tubo ca. 1.5 mm longo, tepalis 6–7 mm longis, filamentis aequalibus, antheris ca. 2 mm longis.

Plants 6–12 cm high. *Corm* globose, 3.5–5 mm diam., tunic layers brown, more or less imbricate, soft-textured, incised above and below. *Cataphyll* membranous, often fragmented. *Leaves* 3 or 2, linear to falcate, to 1 mm wide, oblong in section with margins and midrib strongly thickened, thus narrowly 2-grooved on each surface, the lowermost leaf basal, longest, the second also basal, but sheathing the lower half of the stem and free only above, the uppermost inserted on the upper third of the stem and sheathing for at least half its length (occasionally entirely sheathing and bract-like). *Stem* erect, minutely ciliate, unbranched, flexed above the sheathing part of the upper leaf. *Spike* 1–4-flowered, flexuose; *bracts* 4–5 mm long, green below, membranous to dry and transparent above. *Flower* stellate, white, turning purplish on fading; *perianth tube* ca. 1.5 mm long, not exserted from the bracts, widening from the base; *tepals* 6–7 mm long, obovate, to 3 mm wide. *Filaments* equal, ca. 2.5 mm long; *anthers* ca. 2 mm long, yellow. *Ovary* ca. 1.5 mm long, *style* branching at the apex of the anthers, branches ca. 1.3 mm long, recurved. *Capsule* globose, 3–4 mm long, shorter than bracts. *Chromosome number,* $2n = 26$ (*Goldblatt 5144*).

Flowering time. November.

Distribution. Cedarberg, above 1,400 m, in sheltered wet mossy places on cliffs and cracks in rocks, mainly south-facing. Figure 70.

Geissorhiza ciliatula is a dwarf, white-flowered species from the Cedarberg and Cold Bokkeveld Mountains. In the Cedarberg it grows on the rocky peaks that rise above Middelberg Plateau. It grows in sheltered cracks in south-facing cliffs or under boulders, where shade and water are available late in the growing season. It occurs together with the very different and distinctive large pink-flowered *G. cedarmontana* in a habitat also shared with moss and *Drosera* sp., and occasionally *Hesperantha cedarmontana,* which flowers earlier in the season.

The exact nature of the corm tunics of *Geissorhiza ciliatula* is difficult to determine, as the tunics are soft-textured and not firmly fixed in position. However, they appear to be more or less imbricate and resemble those found in subgenus *Geissorhiza* section *Monticola.* Tentatively, I suggest that *G. ciliatula* may be related to the *G. ramosa* alliance, perhaps closest to the fairly small and also ciliate leaved *G. scopulosa* which occurs in similar habitats in the Hex River Mountains, some distance to the south.

Specimens examined. SOUTH AFRICA. CAPE: 3219 (Wuppertal) Cedarberg, S slopes of Middelberg Central (AC), *Goldblatt 5144* (K, MO, NBG, S); Bokkeveld Sneeuberg, 4,500–5,000 ft., seasonally damp narrow ledges below high cliffs (CD), *Esterhuysen 36127* (BOL, K, MO, PRE, STE).

67. Geissorhiza pseudinaequalis Goldbl., sp. nov. TYPE: South Africa. Cape: Witteberg, Slanghoek Mts., wet overhung cliffs on S side, *Esterhuysen 22293* (holotype, BOL; isotypes, K, MO). FIGURE 71.

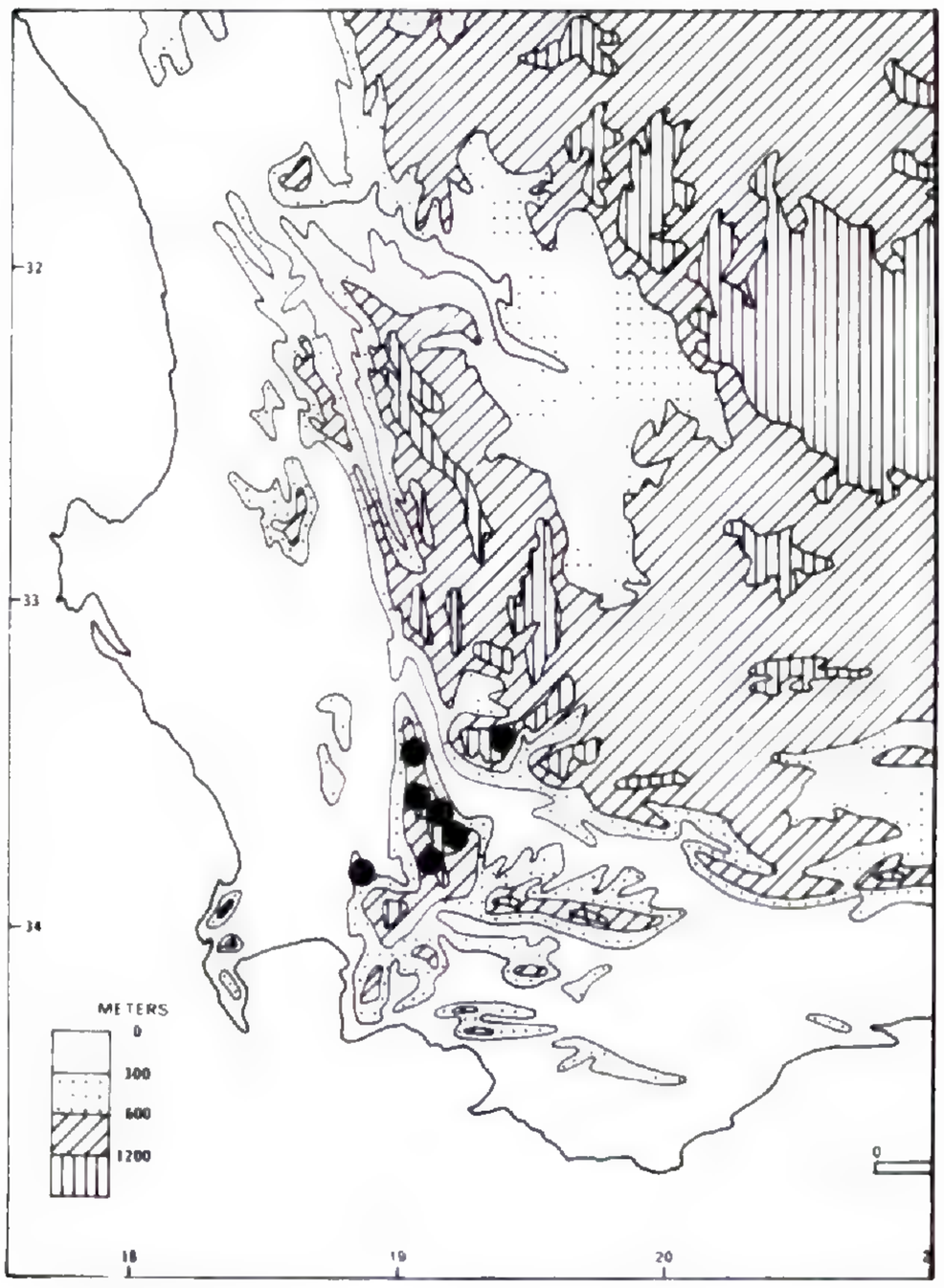


FIGURE 71. Morphology and distribution of *Geissorhiza pseudinaequalis*. Habit ×0.5; flower life size (*Esterhuysen 35281*, Simonsberg).

Planta 9–18(–30) cm alta, tunicis cormi membranoso-papyraceis, imbricatis, foliis 3(–4) planis marginibus costoque parum incrassatis raro sparsim ciliatis, inferioribus 2(–3) basalibus, superioribus infra caulem vaginantibus, caule erecto, spica (2–)3–7 florum, floribus stellatis caeruleo-violaceis, tubo 3–5 mm longo, tepalis 12–17 mm longis, filamentis inaequalibus longioribus duobus 8–10(–12) mm longis, breviore 4–6 mm longo, antheris 3.5–5 mm longis.

Plants 9–18(–30) cm high. *Corm* globose, symmetric, 5–9 mm diam., usually heavily bulbiferous at base, tunics membranous-papery, more or less imbricate, incised below, light brown, the outer layers becoming irregularly broken. *Leaves* usually 3 (or 4), with a sheathing stem bract as well, linear, plane, the margins and midrib slightly raised, occasionally sparsely ciliate on the edges, 2–4 mm wide, usually about as long as the stem, the lower two (or three) leaves basal, the uppermost inserted in the lower to mid part of the stem, and sheathing below. *Stem* erect, smooth, bearing 1 or more sheathing, herbaceous bracts in the upper part, and often branching at this point, and sometimes also from the axil of the upper leaf. *Spike* (2–)3–7-flowered, flexed at the base and flexuose; *bracts* 7–10 mm long, herbaceous, membranous on the upper margin, occasionally becoming dry above, and rarely somewhat tawny. *Flowers* stellate, blue to violet (or mauve) and usually pale in the tube, the throat sometimes ringed with darker color; *perianth tube* 3–5 mm long, not reaching the apex of the bracts; *tepals* 12–17(–20) mm long, obovate, 5–6.5 mm wide. *Filaments* unequal, the two longer 8–10(–12) mm long, the shorter 4–6 mm long; *anthers* 3.5–5 mm long. *Ovary* 2–3 mm long, *style* dividing near or beyond the apex of the anthers, branches recurved. *Capsule* unknown. *Chromosome number,* unknown.

Flowering time. Mid-October to January.

Distribution. Mid to upper elevations in the western Cape mountains between Ceres and Si-

monsberg, on damp, sheltered, south- or west-facing rock ledges and cliffs. Figure 71.

Geissorhiza pseudinaequalis is one of several species of *Geissorhiza* that occupy specialized niches in the southwestern Cape mountains. This species has a limited range from the Hex River Mountains and Bains Kloof to Simonsberg, and apparently grows in rocky places, on ledges, or cracks in cliffs where shade and moisture are available in mid summer, and it may bloom as late as January at higher elevations.

It has often been confused with *Geissorhiza inaequalis* (section *Planifolia*) on account of its markedly unequal stamens and flat leaves. The corms, however, are quite different, *G. inaequalis* having woody, imbricate tunics, smaller flowers and in addition, distinctively puberulent stems. *Geissorhiza pseudinaequalis* has papyraceous corm tunics, relatively large flowers and smooth stems. These two species are probably not closely allied and are here assigned to different sections of subgenus *Geissorhiza*. *Geissorhiza pseudinaequalis* is probably related to other montane species with similar soft-textured imbricate corm tunics such as *G. burchellii* and *G. tabularis*. These two species also have unequal stamens but differ in their larger size and leaves with strongly raised margins and midribs.

The single collection from the Hex River Mountains, *Esterhuysen 15882* at BOL, is mixed, and perhaps partly hybrid. It consists of a specimen of *Geissorhiza heterostyla* with its characteristic small flowers and brown stem bract, several specimens of *G. pseudinaequalis*, and some putative hybrids with flowers of intermediate size and partly brown stem bracts. The leaf margins and midrib of plants of this collection are minutely ciliate, also a feature of *G. heterostyla*.

Specimens examined. SOUTH AFRICA. CAPE: 3318 (Cape Town) Simonsberg, kloof on W side near Helshoogte (DD), *Esterhuysen 35281* (BOL, K, MO, PRE).

3319 (Worcester) Prospect Peak, Hex River Mts., side of waterfall on E slopes (BC), *Esterhuysen 15882* (BOL, NBG, PRE); Bains Kloof, along road 2–3 mi. from hotel (CA), *Esterhuysen 32722* (BOL, PRE, S); Bains Kloof, *L. Bolus s.n.* (BOL 31895, 31909), *Johnson 1* (MO), *Barker 4279* (NBG), *Goldblatt 457* (BOL), *679* (BOL); Upper Wellington Sneeukop, ledges on W side, *Esterhuysen 26546* (BOL, MO); Witteberg, Slanghoek Mts., wet overhung cliffs on S side, *Esterhuysen 22293* (BOL, K, MO); Witteberg, in horizontal and vertical cracks in S-facing ledges, *Esterhuysen 22293A* (BOL, K, PRE); kloof between Molenaarsberg and Witteberg, Du Toits Kloof, *Esterhuysen 24150* (BOL); mts. S of Wemmershoek (CC), *Andreae 821* (PRE).

SECTION *PLANIFOLIA*

11. Section **Planifolia** Goldbl., sect. nov. TYPE: *G. aspera* Goldbl.

Tunicae cormi durae lignosae, foliis plerumque 3, ensiformibus ad linearibus planis, caule puberulo-ciliato, bracteis infra herbaceis supra siccis ferrugineis, floribus actinomorphis stellatis vel declinatis, tubo brevi, staminibus aequalibus vel inaequalibus.

Corm tunics, blackish, hard and woody, *leaves* usually 3, blade plane and smooth, lanceolate to ensiform, rarely linear, *stem* puberulous-ciliate, *bracts* herbaceous below, dry and ferrugineous in the upper half, *flowers* stellate and actinomorphic or declinate, the tube short, stamens equal to unequal.

Species. 4.

68. Geissorhiza aspera Goldbl., J. S. African Bot. 36: 303. 1970. TYPE: South Africa. Cape: Rondebosch common, *Goldblatt 501* (holotype, BOL; isotypes, K, NBG, PRE). FIGURE 72.

Ixia secunda de la Roche sensu Berg., Pl. Cap. 6, 360. 1767; sensu Thunb., Diss. de *Ixia* no. 7. 1783 non *I. secunda* de la Roche (= *G. eurystigma* L. Bolus).

Ixia secunda Ker sensu Ker, Bot. Mag. 17: tab. 597. 1802 (November), hom. illeg. (type of *I. secunda* de la Roche specifically excluded), et nom. superfl. pro *I. pusilla* Andr. (1802, August).

Geissorhiza secunda Ker, Ann. Bot. (König & Sims) 1: 224. 1804; Baker, Handb. Irid. 154. 1892, Fl. Cap. 6: 69. 1896, excl. vars.; Foster, Contr. Gray Herb. 135: 41. 1941 [as *G. secunda* (Berg.) Ker]. TYPE: (illustration in Bot. Mag. 17: tab. 597. 1802).

Gladiolus junceus Burm. f., Fl. Cap. Prod. 2. 1768, nom. nud.

Plants 8–35 cm high. *Corm* ovoid-globose, 3–6 mm diam., tunics dark, often blackish, imbricate. *Leaves* usually 3, flat, linear to ensiform, erect to falcate, the margins and midrib slightly raised, smooth or sparsely puberulent-ciliate, about as long as the stem or somewhat longer, 2–5(–7) mm wide, the lower two basal, the upper basal or inserted shortly above the ground and sheathing the lower part of the stem. *Stem* inclined or erect, simple, more often 1–3-branched, densely puberulent (rough to touch), usually bearing a short leafy bract from the upper node. *Spike* (1–)2–7-flowered, usually flexed below the first flower and secund; *bracts* herbaceous below, dry and brown in the upper half, 6–12 mm long, spreading above, the inner smaller, 6–8 mm long. *Flower* stellate, usually deep blue to purple, occasionally white or pale bluish; *perianth tube* 1–

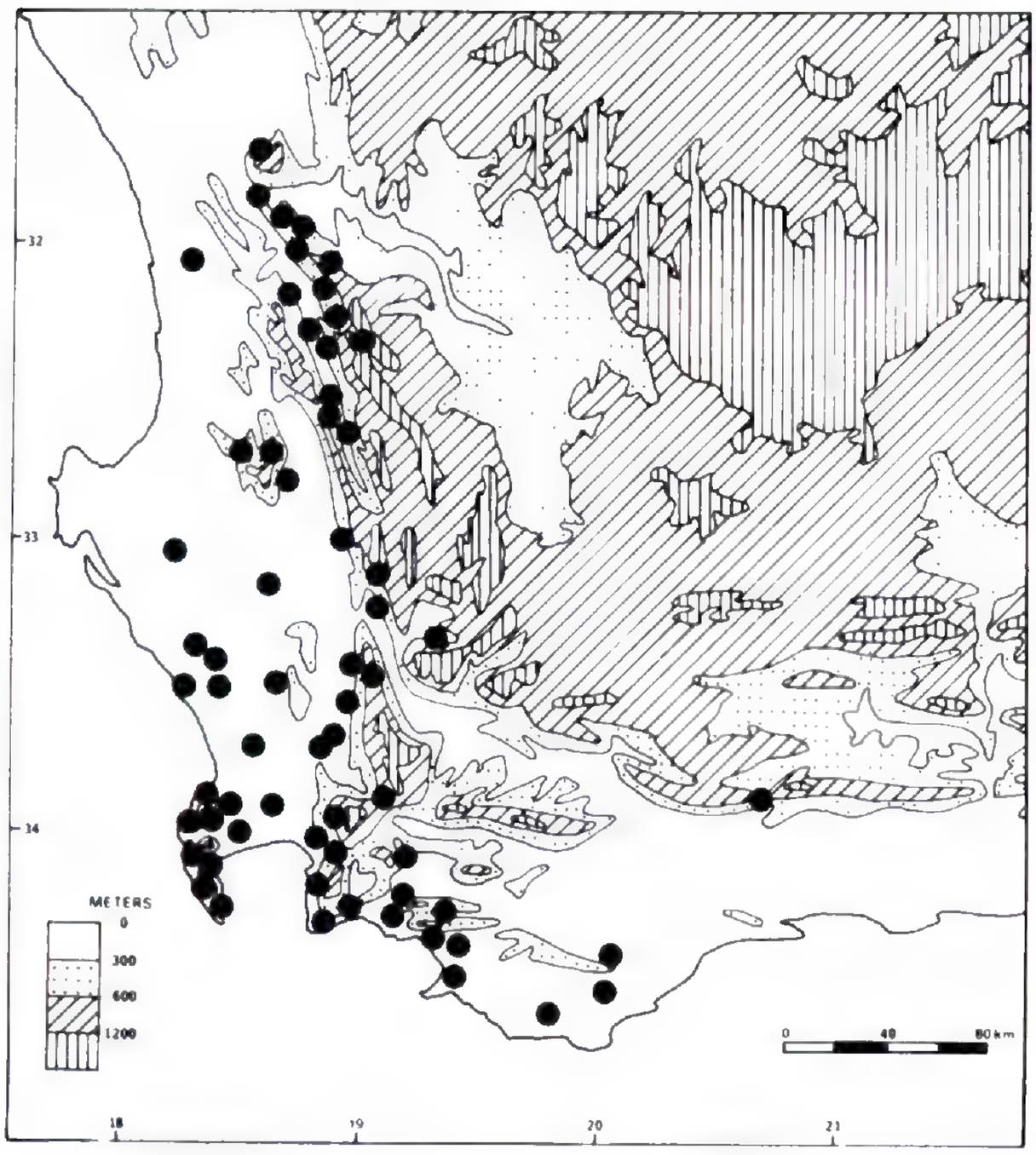


FIGURE 72. Morphology and distribution of *Geissorhiza aspera*. Habit ×0.5; corm and flowering spike life size (*Goldblatt 6274*, Commonage at Malmesbury).

2 mm long, infundibuliform; *tepals* 11–15 mm long, 4–6 mm wide. *Filaments* 3–5 mm long, one sometimes shorter by up to 1 mm; *anthers* erect, 3–5.5 mm long, white to pale yellow. *Ovary* 1.5–2 mm long, *style* 7–8 mm long, branches to 2 mm long. *Capsule* 5–6 mm long, ovoid to rotund. *Chromosome number*, $2n = 52$ (*Goldblatt 213, 520, 4839A, s.n.* no voucher, St. James, Cape Peninsula), $2n = 26$ (*Goldblatt 5350, 5647, s.n.* no voucher, Burghers Pos, Darling).

Flowering time. August to September.

Distribution. Widespread, Cape Peninsula east to the Langeberg at Tradouw Pass and north into the Olifants River Valley as far as the Doorn River and Gifberg. Figure 72.

Geissorhiza aspera is a common southwestern Cape species. It is most often found on sandy soils, but also light clay or granitic ground, both on mountains and flats, and it typically grows in large numbers. It is persistent and is often one of the last survivors of the native flora after severe disturbance. Plants vary greatly in size, depending on soil fertility and the amount of moisture available, and may grow well over 30 cm high, or be stunted and less than 10 cm. The flowers are deep glistening blue to mauve in the southwestern Cape, but occasional white mutants occur, sometimes even in pure colonies. It is more frequent in the south, in the Caledon district, on the Cape Peninsula and locally to the north, around Darling and Malmesbury, but it extends north through the Olifants River Valley and Cedarberg Mountains to the Gifberg Mountains near Van Rhynsdorp. Here *G. aspera* is more variable, and plants with white to pale bluish flowers rather than the typical dark blue-purple are frequent. In the north of its range plants are often found in sheltered sites, sometimes in the lee of rocks or on moister south trending slopes. The stamens are often described as being equal (Foster, 1941), but careful examination of live

plants shows that one filament is usually slightly shorter, and in populations in the north of its range the filaments are distinctly unequal. *Geissorhiza aspera* is unusual in the genus in being heteroploid with both diploid, $2n = 26$, and polyploid, $2n = 52$, populations. From the sample of seven populations so far counted, there is a pattern of diploids in the north of the range and tetraploids in the south, but both cytotypes have been recorded on the Cape Peninsula.

Geissorhiza aspera is closely allied to *G. inaequalis,* a more robust species, which has large pale blue-mauve flowers. It shares with *G. aspera* the characteristic puberulous stem and broad flat leaves. In *G. inaequalis,* the short filament is about half as long as the others and the bracts are green to membranous during flowering and unlike the typical dry, brown-tipped bracts of *G. aspera.*

The nomenclature of this common species is unfortunately complex and confusing. Its history begins when Bergius published a description of a plant he called *Ixia secunda* in his "Plantae Capensis" in 1767, based upon specimens in his collection in Stockholm. However, in the addendum to this work he cites *I. secunda* de la Roche (1766), in effect, but perhaps not by intention as a synonym. Bergius' *I. secunda* is regarded here as having no nomenclatural validity, but is merely a misapplied name. *Ixia secunda* de la Roche is the species currently known as *G. eurystigma* (Goldblatt, 1983). De la Roche's study of Cape Iridaceae, published in 1766, was largely misunderstood by contemporary and succeeding botanists and the name *I. secunda* was usually applied to plants matching Bergius' description and specimens (e.g., Thunberg, 1783; Ker, 1802a, 1802b), and this situation led to considerable nomenclatural confusion when the two species named *Ixia secunda* were transferred to *Geissorhiza.*

Ker, who actually understood that *Ixia secunda* de la Roche and *I. secunda* sensu Bergius were different species, published descriptions and illustrations of both in Curtis' "Botanical Magazine." He renamed what he thought was *I. secunda* de la Roche (i.e., the earlier epithet) *I. rochensis,* citing of course *I. secunda* de la Roche as a synonym. This name is therefore, nomenclaturally superfluous. It has, unfortunately, been applied in Ker's sense ever since to the well known Cape species, now to be called *G. radians* (Thunb.) Goldbl.

Ker (1802b) named the small, blue-flowered and pubescent stemmed plant *Ixia secunda* citing, of course, *I. secunda* sensu Bergius, but excluding de la Roche's species. According to current rules of nomenclature, Ker's *I. secunda* is a new name and a homonym for *I. secunda* de la Roche. It is also superfluous, since *I. pusilla* Andr. was cited as a synonym. Upon transfer to *Geissorhiza, G. secunda* cannot be treated as a legitimate new name in terms of article 72.2 as it is still superfluous, *I. pusilla* not having been excluded when the transfer was made. The new name *G. aspera* was provided by myself (Goldblatt & Barnard, 1970) for *G. secunda* Ker and as the only legitimate synonym, the name must be used for this well known Cape plant (Goldblatt, 1983).

Specimens examined. SOUTH AFRICA. CAPE: 3118 (Van Rhynsdorp) near Doorn River bridge, old road between Clanwilliam and Van Rhynsdorp (DC), *Goldblatt 3866* (MO); Gifberg, *Compton 20848* (NBG), *Barker 9594* (NBG, UC), *Phillips 7523* (NBG, in part), *7520* (NBG); Gifberg, E slopes of plateau, *Esterhuysen 21947* (BOL); Nardouw Kloof (DD), *Stokoe s.n.* (SAM 59842); Bulshoek Barrage, *Barker 9062* (NBG).

3218 (Clanwilliam) between Graafwater and Lamberts Bay (AB-BA), *L. Bolus s.n.* (BOL 23185); 9 mi. S of Clanwilliam (BB), *Lewis 5209* (M, NBG); Clanwilliam, *Loubser 938* (NBG); Olifants River Dam, Clanwilliam, *Steyn 513* (NBG); 10 mi. N of Clanwilliam (BB), *Barker 3613* (NBG); 20 mi. N of Citrusdal, Olifants River Valley, *Lewis 1033* (SAM); Kransvlei Berg, *Barker 5338* (NBG); pass over Kransvlei Mts., *Lewis 1870* (SAM); 8 mi. S of Clanwilliam, *Goldblatt 266* (BOL); 14 km S of Clanwilliam, *Goldblatt 2472* (MO, US); between Clanwilliam and Algeria, *Goldblatt 2569* (MO, PRE, S); Olifants River Valley, N of Rondegat, *Goldblatt 5647* (MO, NBG, S, US, WAG); Kapteins Kloof (DA), *van Niekerk 636* (BOL); Modderfontein, Olifants River (DB), *Diels 209* (B); Greys Pass, *Lewis s.n.* (K), *Hafstrom & Acocks 298* (PRE, S); near Piketberg (DC), *Barnes s.n.* (BOL 31899), *Barker 7564* (MO, NBG); Levant Peak, *Marloth 11528* (BOL), *Esterhuysen s.n.* (MO).

3219 (Wuppertal) Pakhuis Pass (AA), *Bond 590* (NBG); Middelberg, Cedarberg, shady rocky crevices (AC), *Compton 6613* (NBG); Cedarberg, Uitkyk Pass, *Gillett 4113* (MO); Warm Baths (CA), *Leipoldt s.n.* (BOL 31901); Waterfall River, Citrusdal, *Barker 3775* (NBG); Platkloof, *Hanekom 1236* (STE).

3318 (Cape Town) near Hopefield (AB), *Bachmann 217* (Z); Darling (AD), *Bachmann 519* (B), near Darling, *Stokoe s.n.* (SAM 49601), *Grant 2532* (MO); 4 mi. N of Mamre, *Lewis 1040* (SAM); Groenekloof, *Zeyher s.n.* (SAM 20838, 20839), *Ecklon & Zeyher Irid. 228* (B, SAM), *MacOwan 2165* (K, SAM), *H. Bolus 4338* (BOL, K); Mamre Hills, *Barker 1475* (NBG); Waylands, Darling, *Barker 807* (NBG); veld near Darling, *Lewis 2532* (MO); Moorreesburg (BA), *Bachmann 1089* (B, Z); Tulbagh road near Porterville (BB), *Wilman 715* (BOL); Porterville, *Steyn 583* (NBG); Malmesbury commonage, on S slope of hill (BC), *Gold-*

blatt 6274 (MO, WAG); flats N of Hermon (BD), *Goldblatt 6411* (MO); Bok Point (CB), *Barker 806* (NBG); Hof Str, Cape Town (CD), *Page s.n.* (BOL); Signal Hill, *Penfold s.n.* (SAM 52898), *Barker 406* (NBG), *703* (NBG), *Wilms 3739* (B), *Dümmer 886* (E), *Salter 531* (K); Lions Head, *MacOwan s.n.* (SAM), *Marloth 7394* (PRE), *Schlechter 1579* (B, FI, G, W, Z); Signal Hill, W slopes, *Goldblatt 213* (BOL), Camps Bay, lower slopes, *Cassidy 250* (BOL); lower Blinkwater, *Cassidy 12* (BOL, NBG); near Rosebank, *H. Bolus 4804* (BOL, K); W slopes of Orange Kloof, *Wolley Dod 3453* (BOL); Rondebosch common, *Goldblatt 501* (BOL, K, NBG, PRE); Camp Ground, *H. Bolus 4609* (BM, BOL, GH, K, Z); Bergplatze bei Capstadt, *Ecklon & Zeyher Irid. 228* (64.9) (B, FI, G, GH, L, LD, MO, W, Z); slopes of Table Mt., *MacOwan in Herb. Norm. Aust. Afr. 807* (B, BM, BOL, G, SAM, Z); Table Mt., *Zeyher 5034* (SAM), *Ecklon 310* (B, BM, E, G, K, M, S, Z), *Rogers 16973* (PRE, Z); Salt River, *Zeyher 70* (BOL, SAM); near Wellington (DB), *L. Bolus s.n.* (BOL 31900), *Moss 4307* (J); Paarl Mt., *Henderson 1184* (NBG), *Drège 8483a* (B, BM, G, K, L, MO); between Paarl and Pont, *Drège s.n.* (SAM 20842), *Drège 8483c* (B, G, K, L, MO); Dal Josaphat, *Grant 2340* (BOL, MO, P); Langverwacht, above Kuils River (DC), *Oliver 4710* (PRE, STE); Jonkershoek Valley (DD), *Lewis 1611* (SAM); Swartbos Kloof, Jonkershoek, *Lewis s.n.* (SAM 58954); Klapmuts, *Lewis 4451* (NBG); Stellenbosch, *Prior s.n.* (K), *Garside 1067* (K).

3319 (Worcester) lower slopes, Great Winterhoek Mts. (AA), *Thorne s.n.* (SAM, PRE); Tulbagh (AC), *Kassner 1306* (BR, E), *Garside 1544* (K); Lakenvlei (BC), *Barker 1474* (NBG); Bains Kloof (CA), *Lotsy & Goddijn 879* (L); French Hoek Pass (CC), *Werdemann & Oberdieck 381* (B, K, PRE), *Boucher 2347* (K, PRE).

3320 (Montagu) foot of Tradouw Pass (DC), *Marsh 878* (STE).

3418 (Simonstown) Simonstown (AB), *Wolley Dod 582* (BOL); between Witsands and Redhill, *Lewis 1074* (SAM); Chapmans Peak, *van Niekerk 465* (NBG); Redhill, W slopes, *Barker 5912* (NBG); Simons Bay, *Wright s.n.* (K, L); Grasslands Kloof, Cape Point Reserve (AD), *Taylor 8620* (STE); Cape Flats (BA), *MacOwan s.n.* (SAM 48596), *Krauss 1394* (MO), *Rehmann 1837* (BM, BR, Z), *Marloth 7261* (PRE); Helderberg (BB), *Parker 4257* (GH, K, NBG, PH, PRE); Sir Lowrys Pass, *Schlechter 1579* (B); near Somerset West, *Ecklon & Zeyher Irid. 226* (B, FI, K, LD, MO, SAM); Pringle Bay, Hangklip (BD), *Gillett 4204* (BOL); Palmiet River mouth, *Gillett 4241* (BR, LD, MO); Kogel Bay, *Werdermann & Oberdieck 288* (B, BR, K, PRE, WAG).

3419 (Caledon) 8 mi. N of Bot River (AA), *Goldblatt 293* (BOL); quarry above Onrus (AC), *Horocks 19* (MO); Albertyn-Caledon road, Avontuur farm, *Goldblatt 4981* (MO); Hemel-en-Aarde (AD), *Gillett 1403* (BOL, STE); Fernkloof, Hermanus, *Goldblatt 5178* (MO, PRE), *Orchard 281* (BR, E, K, STE); Vogelklip, Hermanus, *Barker 1788* (NBG); Stanford, *Gillett 4449* (BR, MO); Genadendal (BA), *Kogel s.n.* (B); Fransche Kraal, Waterfall (CB), *Barker 7554* (NBG); Groot Hagelkraal, limestone boulders and cliffs (DA), *Oliver 6142* (PRE, STE); The Poort, Bredasdorp (DB), *Dymond s.n.* (BOL 31899); roadside between Hermanus and Stanford, *Gillett 4512* (BOL, PRE);

3420 (Bredasdorp) near Bredasdorp (CA), *Sidey 1831* (MO, S); Swellendam, Buffeljagsrivier, farm Middenplaas (BA), *Vlok 325* (MO).

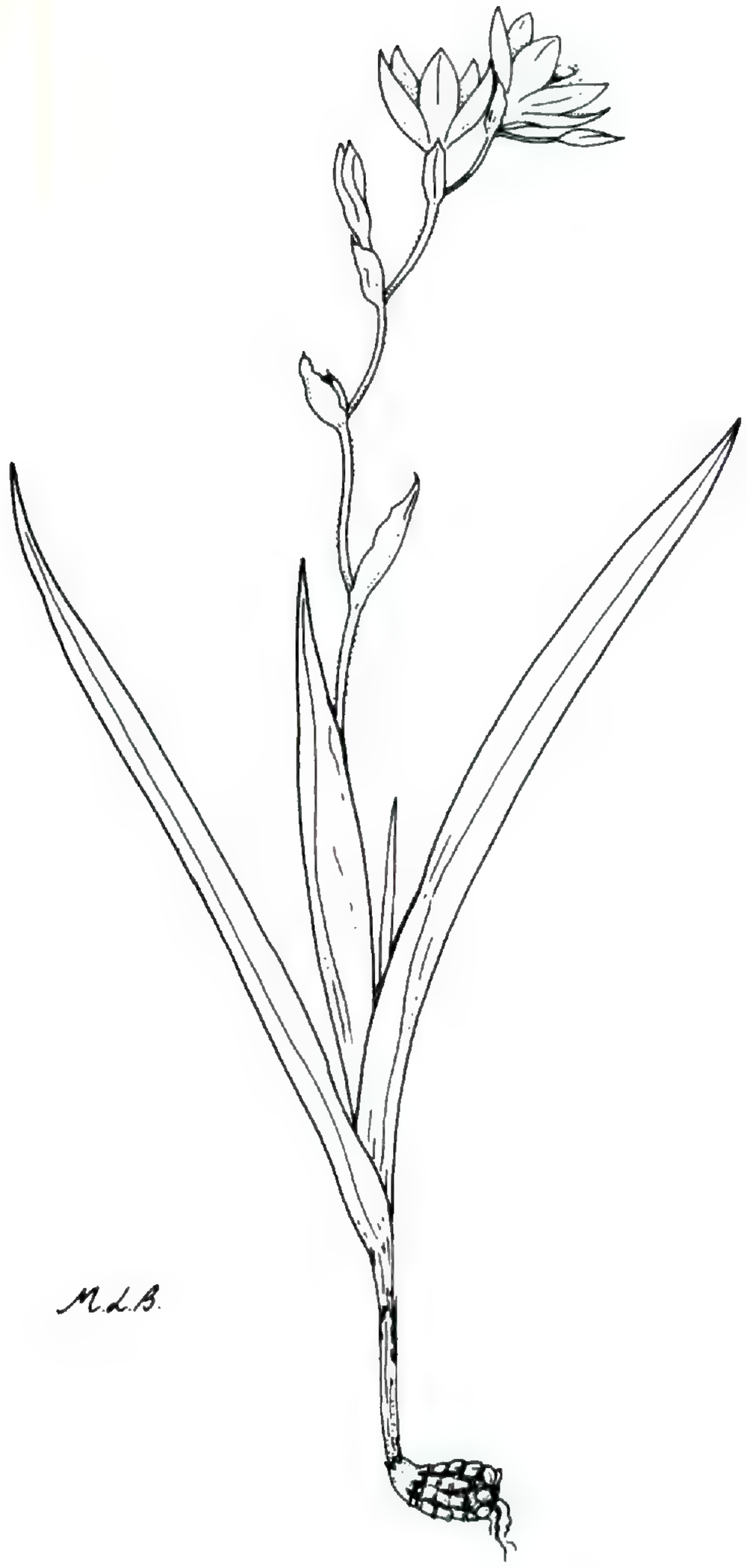
WITHOUT PRECISE LOCALITY: Cape of Good Hope (CBS), *Lalande s.n.* (B, P), *Lichtenstein s.n.* (B), *Bergius s.n.* (B), *Mund & Maire s.n.* (B), *Harvey 867* (E), *876* (E), *Commerson s.n.* (G), *Niven s.n.* (BR), *Verreaux s.n.* (G), *Bowie 403* (G), *Alexander s.n.* (BR, Z), *Thunberg s.n.* (S, UPS), *Grondal s.n.* (S); "Olifants R. bei villa Brakfontein," *Ecklon & Zeyher Irid. 213* (76) (B, SAM); banks of Olifants River, *Schlechter 5029* (B, BM, BR, E, G, GH, K, P, S, STE, Z); Herb. Burman *s.n.* "*Gladiolus junceus*" (G); Olifantsrivier, *Penther 666* (Z), *679* (Z).

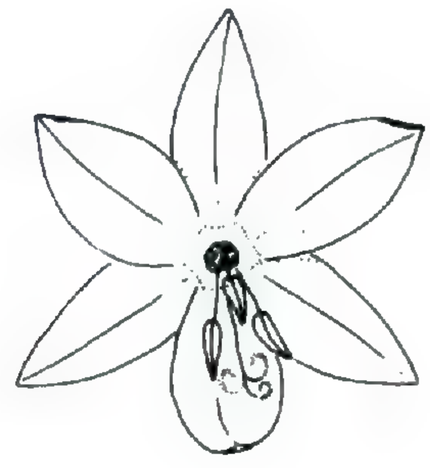
69. Geissorhiza inaequalis L. Bolus, S. African Gard. 20: 346. 1930; Foster, Contr. Gray Herb. 135: 45–46. 1941. TYPE: South Africa. Cape: Klipkoppies 6 mi. from Nieuwoudtville, *L. Bolus s.n.* (lectotype, BOL 19256, here designated; isolectotypes, BM, BOL, K). FIGURE 73.

Plants 12–25 cm high. *Corm* ovoid-globose, 6–8 mm diam., tunics dark, often blackish, imbricate, bearing several cormlets around the base. *Leaves* usually 3, flat, ensiform, erect to falcate, margins and midrib slightly raised, smooth, shorter to somewhat longer than the stem, 4–10 mm wide, the lower two leaves basal, the third basal or inserted above the ground and sheathing for some distance. *Stem* more or less erect, simple or 1–3-branched, lightly papillose-puberulent, usually bearing a short leafy bract from the upper node. *Spike* 2–7-flowered, usually flexed below the first flower and secund; *bracts* herbaceous below, drying and becoming pale and membranous above, rarely brownish at apex, 10–15(–18) mm long, spreading in the upper half, the inner bract shorter than the outer. *Flower* stellate, pale blue-mauve, whitish in the center; *perianth tube* 2–3 mm long, infundibuliform; *tepals* 20–23 mm long, 4–6 mm wide. *Filaments* unequal, the two longer 8–10 mm long, the shorter 5–6 mm long, nearly horizontal and initially more or less unilateral; *anthers* inclined to horizontal, 5–6 mm long, one sometimes slightly shorter, white. *Ovary* 2–3 mm long, *style* dividing near the apex of the anthers, branches ca. 3 mm long, recurved. *Capsule* oblong, 5–8 mm long, ca. 3.5 mm wide, shorter than the bracts. *Chromosome number*, $2n = 52$ (*Goldblatt 129, 275*).

Flowering time. Late August to early October.

Distribution. Heavy soils in the Nieuwoudtville district, often in rocky situations. Figure 73.





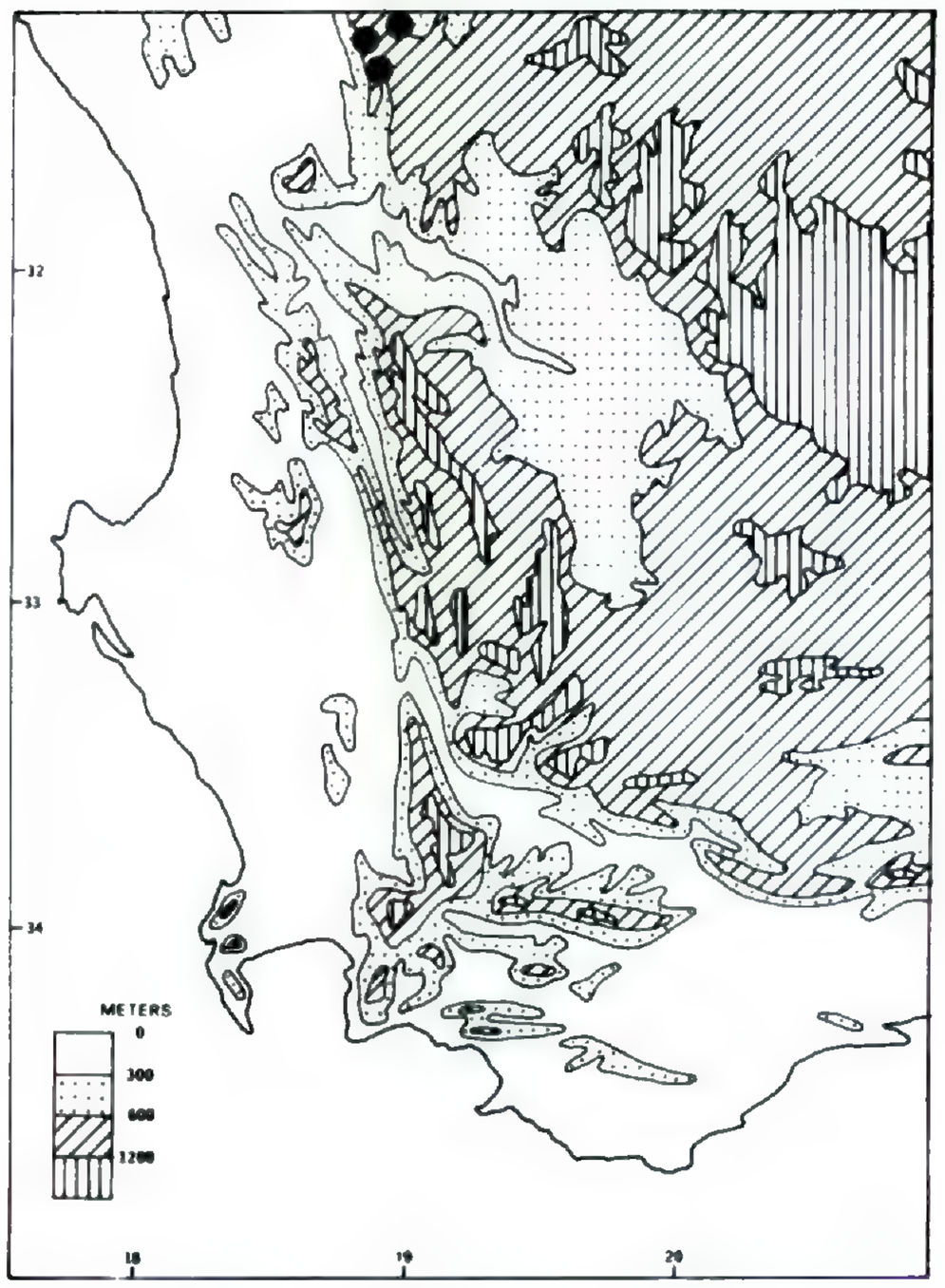


FIGURE 73. Morphology and distribution of *Geissorhiza inaequalis*. Habit ×0.5; flower life size [Nieuwoudtville Reserve (ex hort.), no voucher].

Geissorhiza inaequalis is most closely related to the very common and widespread *G. aspera* (syn. *G. secunda*) and it is sometimes difficult to distinguish them when dry. Both have a similar habit, flat ensiform leaves and puberulent stems. *Geissorhiza aspera* typically has deep blue-violet, less often whitish, flowers and at flowering time the upper parts of the floral bracts are often dry and rusty brown. It usually has equal or subequal stamens, but populations with one shorter stamen are not uncommon. In contrast, *G. inaequalis* has larger, pale blue-mauve flowers, typically green or pale, membranous bracts at flowering time, the brown coloration developing only after the flowers fade. It also has one filament about half as long as the others and even one anther may be slightly shorter then the other two. In *G. inaequalis*, the stamens are inclined to horizontal and nearly unilateral while they are erect and symmetrically disposed in *G. aspera*. *Geissorhiza inaequalis* may also be confused with *G. heterostyla* L. Bolus [syn. *G. rosea* (Klatt) Foster], which is similar in habit, and has one short filament. The latter, however, has leaves ciliate on raised margins and midrib, usually a glabrous stem and it typically has a short dry bract leaf in the upper part of the stem. Dry material must be examined carefully to avoid misidentification.

The species is unusual in the genus in being tetraploid, $2n = 52$. It is restricted to heavier soils

in the Nieuwoudtville district where it occurs at the edge of the Karoo, often in rocky sites.

Specimens examined. SOUTH AFRICA. CAPE: 3119 (Calvinia), Klipkoppies, ca. 6 mi. from Nieuwoudtville (AC), *L. Bolus s.n.* (BM, BOL 19256, K); Glenlyon farm, Nieuwoudtville, *Oliver & Mauve 30* (PRE, STE); near the top of Van Rhyns Pass, *Goldblatt 269* (BOL); Grasberg road, 4 mi. from Nieuwoudtville, *Goldblatt* 275 (BOL); 5 mi. from Nieuwoudtville, *Barker 9560* (NBG); Nieuwoudtville Reserve, among dolerite boulders in red clay, *Perry & Snijman 2360* (NBG); Uitkomst farm, SW of Nieuwoudtville (CA), *Barker 10733* (NBG).

70. Geissorhiza monanthos Ecklon, Topogr. Verz. Pflanzensamml. Ecklon 21. 1827; Baker, Fl. Cap. 6: 71. 1896, in syn. sub *G. rochensis*; Foster, Contr. Gray Herb. 135: 39. 1941 [as *G. monantha* (Thunb.) Ecklon]. *Ixia monanthos* Thunb., Fl. Cap. 1st edition (Uppsala), 226. 1811, Fl. Cap. 2nd edition (Copenhagen), 123–124. 1818 (or 1820), hom. illeg. non de la Roche (1766) (= *Sparaxis* sp.). TYPE: South Africa. Cape: exact locality unknown, *Thunberg s.n.* [lectotype, Herb. Thunb. 975 UPS, designated by Goldblatt (1982)]. FIGURE 74.

Geissorhiza bellendenii MacOwan, J. Linn. Soc., Bot. 25: 393. 1890; Baker, Handb. Irid. 156. 1892, Fl. Cap. 6: 72. 1896. TYPE: South Africa. Cape: Groen Kloof, *MacOwan s.n. in Herb. Norm. Austr. Afr. 810* (lectotype, SAM; isolectotypes, B, BM, BOL, G, K, S, SAM).

Geissorhiza rochensis var. *monantha* (Sweet) Baker sensu Baker, Handb. Irid. 156. 1892, Fl. Cap. 6: 71. 1896, excl. basion.

Geissorhiza lewisiae Foster, Contr. Gray Herb. 135: 45. 1941. TYPE: South Africa. Cape: Langebaan, *Lewis s.n.* (holotype, Herb. Bolus 20303 in K; isotype, BOL), syn. nov.

N.B. *Geissorhiza monantha* Sweet (1830) is a different species, based on a different type. It is regarded here as a homonym of *G. monanthos* and is currently known as *G. eurystigma.*

Plants (6–)10–20 cm high. *Corm* globose, symmetric, 5–10 mm diam., usually with many cormlets around the base, tunics imbricate, blackish, layers notched below into regular segments. *Cataphyll* membranous, often evidently lacking. *Leaves* 3–4, more or less erect, linear to ensiform, plane with the midrib distinct, (1–)2.5–4 mm wide, usually slightly shorter than the stem, the lower two leaves basal, the upper cauline, decreasing in size and sheathing below, the uppermost sometimes bract-like, smooth entirely or ciliate to pubescent along the margins and sometimes other main veins. *Stem* erect, flexed at the base of the spike, minutely puberulous, simple or 1–2-branched. *Spike* 1–4(–5)-flowered, flexuose; *bracts* (8–)10–12 mm long, herbaceous in bud, becoming dry and brown above as the flowers open, folded outwards in the upper part, the inner slightly smaller than the outer. *Flower* either dark blue-violet and pale yellow in the center and the tube or sometimes red in the lower part of the tepals, stellate or slightly cupped, zygomorphic with upper tepal tilted downwards, and stamens declinate, held above upper tepal, the style lying under the stamens; *perianth tube* ca. 2 mm long, cylindric; *tepals* obovate, 14–18 mm long, 9–12 mm wide. *Filaments* 6–8 mm long, usually equal, rarely one slightly shorter, declinate, held above the upper tepal; *anthers* unilateral, red-brown or yellow, 4.5–5.5 mm long. *Ovary* ca. 2 mm long, *style* decumbent, lying below the stamens, branching at mid anther level, branches recurved. *Capsule* ovate, 7–8 mm long, enclosed in the bracts. *Chromosome number,* unknown.

Flowering time. Late August to mid-October.

Distribution. Southwestern coastal belt from the foot of the Hottentots Holland Mountains to the Vredenburg-Saldanha area, with outlying populations in the Olifants River Valley near Citrusdal: on sandy or rocky soils, mostly of granitic origin, sometimes growing in cracks in granite rocks. Figure 74.

This relatively common and conspicuous west coast *Geissorhiza* has been known at least since it was collected by Thunberg in the 1770s. It remained undescribed until 1811 when the first edition of Thunberg's "Flora Capensis" was published. Unfortunately the name Thunberg selected, *Ixia monanthos,* was a homonym for a species described in 1766 by Daniel de la Roche, and hence illegitimate. Ecklon's (1827) combination in *Geissorhiza,* based on the Thunberg species can however be regarded as a new name from 1827 [Botanical Code article 72(1), Stafleu 1978)]. Thus the fairly well known name *G. monanthos* can be preserved in its current sense. Much later, in 1890, MacOwan described *G. bellendenii* quite independently, based on plants he collected near Mamre, at Groene Kloof. At the time MacOwan was evidently unaware of the existence of the name *G. monanthos* for this species, and was concerned in drawing attention to the differences between his plant and *G. radians* (then known as *G. rochensis* Ker).

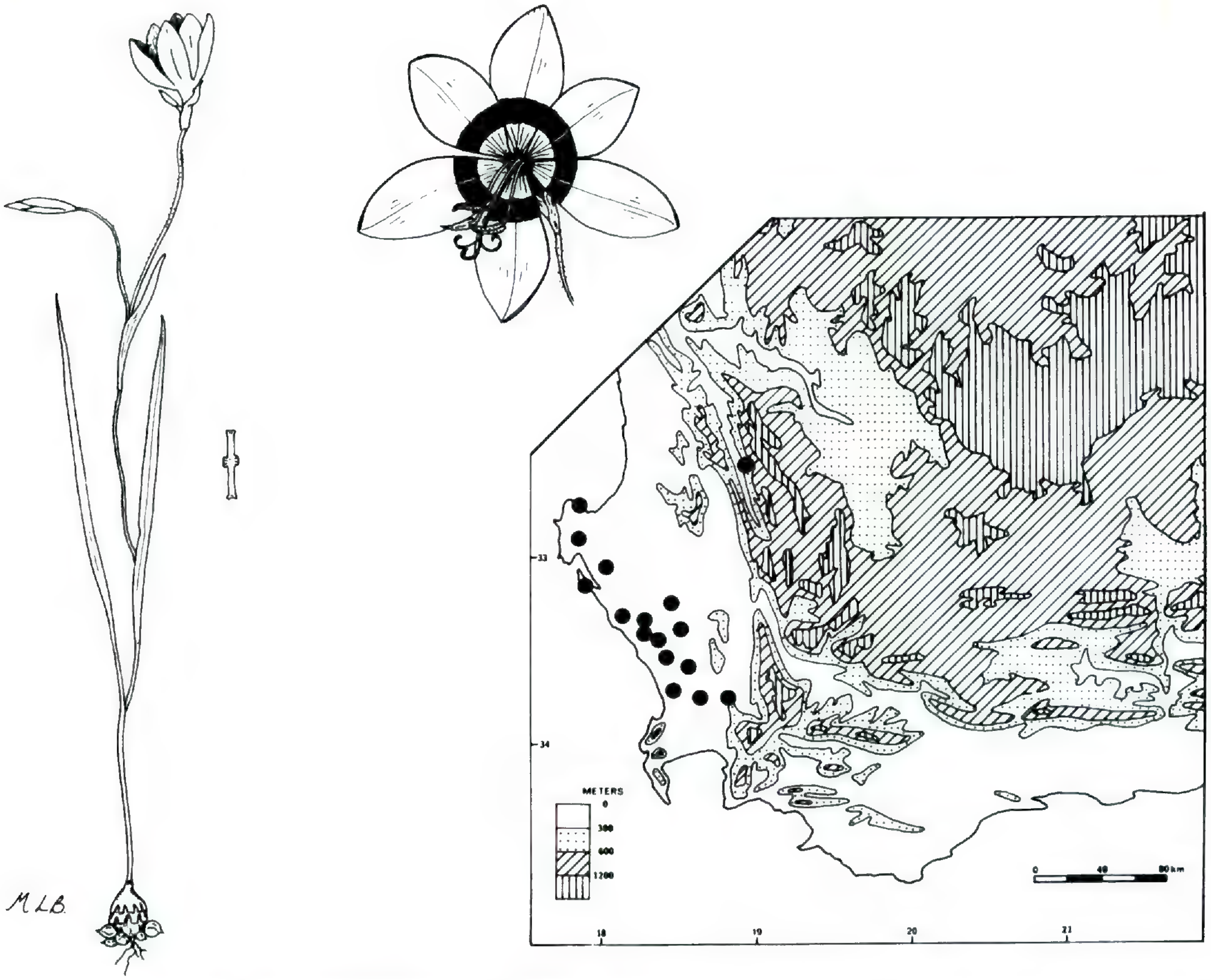


FIGURE 74. Morphology and distribution of *Geissorhiza monanthos*. Habit ×0.5; flower life size; leaf section enlarged (*Goldblatt 6286*, Mud River road, near Darling).

Geissorhiza monanthos is closely allied to *G. aspera* (*G. secunda* sensu auct.), but also resembles fairly closely the unrelated *G. radians*. *Geissorhiza aspera* has a similar puberulous stem and flat leaf lamina, but smaller and actinomorphic flowers, while *G. radians* has the zygomorphic flower found in *G. monanthos*, but different floral markings, a more cupped flower, smooth stem, and narrow 4-grooved leaves, the upper of which has a strongly ribbed sheath.

Plant size and leaf width vary considerably in *Geissorhiza monanthos*. Plants receiving little rainfall or in dry situations are short, with solitary flowered spikes and filiform leaves while plants growing in seasons of generous rainfall or in favored sites can be to 25 cm high with broad leaves and several flowered spikes. A single population can yield plants covering the whole range of variation for these characters (e.g., *Barker 3597, Goldblatt 2705*).

Populations in the Darling-Mamre area have flowers that are blue and red or blue with a yellow center ringed in dark purple (*Margin 1168, Barker 724, Loubser 954, Goldblatt 6286, 6272*), the type of *Geissorhiza bellendenii* matching the blue- and red-colored form. These plants seem to differ in no other way from pure blue-flowered plants and are treated here as the same species. This bicolored flower is like that found in the related *G. radians* with which *G. monanthos* occasionally grows (*Barnard s.n.*, SAM 68439). The similarity is probably an example of color mimicry, a common phenomenon in the Cape flora, or less likely to hybridization and introgression.

Foster (1941) recognized as a distinct species *Geissorhiza lewisiae*, here reduced to synonymy. He distinguished the species on the basis of the type having slightly unequal filaments, and he grouped it with species such as *G. inaequalis* which also has unequal filaments. I have examined the type, collected by G. J. Lewis at Langebaan, and the only collection of *G. lewisiae*

known to Foster and it is clear that one of the filaments is shorter than the other two, but the difference is no more than 0.5 mm, and this small difference can also be detected in several collections of *G. monanthos*. What seems more remarkable about this collection is that the leaves have a conspicuous, fine pubescence on the margins and major veins. This condition is unusual in *G. monanthos* but can be seen in some collections of the species from the north of its range (*Goldblatt 2705, 4084*) where it is developed to a lesser degree. There seems little in fact to distinguish *G. lewisiae* and the species is here reduced to synonymy.

In "Flora Capensis," Baker (1896) treated *G. monanthos* as a variety of *G. radians* (as *G. rochensis*), confusing it with *G. eurystigma* L. Bolus, while recognizing as distinct *G. bellendenii*. There is no doubt that Baker was mistaken in considering this a different species. The confusion is probably based on his inadequate knowledge of the type material of *G. monanthos* rather than any fundamental difference between it and the type of *G. bellendenii*.

Specimens examined. SOUTH AFRICA. CAPE: 3217 (Vredenburg) Witteklip, near Vredenburg (DD), *Lewis 1039* (SAM), *Compton 15915* (NBG), *Leighton 597* (BOL), *Goldblatt 5846* (MO, NBG, US); near Vredenburg, *Lewis 1041* (SAM).

3218 (Clanwilliam) Steenberg Cove (CC), *Lewis 1038* (BOL, PRE, SAM), *Leighton 601* (BOL, K, PRE).

3219 (Wuppertal) 2 mi. N of Citrusdal, Olifants River Valley (CA), *Lewis 1415* (SAM); 5 mi. N of Citrusdal, *Lewis 5201* (NBG), *Compton 20761* (NBG); Citrusdal, *Barker 3597* (NBG).

3318 (Cape Town) Olifants Kop, E of Langebaan (AA), *Goldblatt 2705* (BR, MO, PRE, S, US, WAG); Postberg, *Lewis 5244* (NBG), *Goldblatt 4084* (MO); Langeban, *Lewis s.n.* (BOL 20303, K); Snydersfontein, 2 km NW of Platteklip (AC), *Thompson 3495* (STE); hills around Darling (AD), *H. Bolus 12844* (BR, MO, PRE); Waylands, Darling, *Barker 274* (NBG); Darling commonage, *Barker 8045* (NBG); Darling, *Loubser 954* (NBG), *Stokoe s.n.* (SAM 56869), *Salter 1350* (BM); Darling Hill, *Goldblatt 6272* (MO); granite outcropping, Mud River road, *Goldblatt 6286* (K, MO, PRE); 2 mi. from Darling on Hopefield road, *Barnard s.n.* (SAM 68439); Groen Kloof, *MacOwan s.n. in Herb. Norm. Austr. Afr. 810* (B, BOL, G, K, S, SAM), *H. Bolus 4341* (BOL, K); Oudepost, between Malmesbury and Hopefield (BA), *Salter 3873* (BM, BOL, K); Abbotsdale Station (BC), *Martin 1168* (NBG); 33 mi. N of Cape Town on Malmesbury road (DA), *Gillett 4146* (MO); 5.3 mi. NW of Klipheuwel, *Acocks 20644* (PRE); 0.3 mi. NE of Klipheuwel, *Lewis 4450* (SAM); Phisante Kraal (DC), *Compton 16015* (NBG); Klapmuts, hard sandy ground (DD), *Lewis 4449* (MO, PRE, SAM); Joostenberg, sandy flats, *Lewis 5902* (NBG); Hercules Pillar, *Leighton 556* (BOL, K).

3418 (Simonstown) Hottentots Holland (BB), *Zeyher s.n.* (SAM 20867).

WITHOUT PRECISE LOCALITY: Malmesbury road, *L. Bolus s.n.* (BOL 31902); Cape, *Siebold 577* (B), *Masson s.n.* (BM).

71. Geissorhiza tulbaghensis F. Bolus, Ann. Bolus Herb. 2: 160. 1918; Foster, Contr. Gray Herb. 135: 40–41. 1941. TYPE: South Africa. Cape: Tulbagh, *L. Bolus s.n.* [lectotype, BOL 14851, designated by Foster (1941); isolectotypes, K, PRE]. FIGURE 75.

Plants 6–15 cm high. *Corm* globose, symmetric, truncate at the base, 5–8 mm diam., tunics imbricate, blackish, the outer layers regularly notched below into truncate sections. *Cataphyll* membranous, often broken. *Leaves* 3–4, ensiform to lanceolate, rarely oblong, plane, (1.5–)2–6(–10) mm wide, shorter to slightly longer than stem, often sticky below and with soil adhering, the lower two or three leaves basal, the two lowermost narrow below and often forming a pseudo-petiole, the third sheathing the base of the stem, the uppermost cauline, partly sheathing the stem (sometimes becoming bract-like). *Stem* erect, minutely puberulent, flexed above the leaf sheaths, simple or with 1 or 2 branches from the axils of the cauline or basal sheathing leaf. *Spike* 1, rarely 2-flowered, flexed at the base; *bracts* 10–18 mm long, green below, brown and dry above, the inner shorter than the outer. *Flower* zygomorphic, the stamens unilateral and declinate, held over the horizontal dorsal tepal, the style lying under the stamens, tepals white with maroon-red to brownish markings towards the base; *perianth tube* 4–5 mm long, infundibuliform; *tepals* 18–22 mm long, the outer 10–13 mm wide, the inner 8–11 mm wide. *Filaments* 10–12 mm long, equal, unilateral and declinate; *anthers* 3–4.5 mm long, erect, contiguous, pollen dark red-brown. *Ovary* ca. 4 mm long, *style* declinate, lying under the stamens, branches ca. 5 mm long, recurved. *Capsule* 6–8 mm long, shorter than the bracts, ovate-oblong. *Chromosome number*, $2n = 26 + 1B$ (*Goldblatt 5227*).

Flowering time. August to mid-September.

Distribution. Heavy, often stony clay soil, in renosterbosveld on the flats at the foot of the mountains between Wellington and Porterville, and in the Tulbagh Valley. Figure 75.

Geissorhiza tulbaghensis is one of the most beautiful species of the genus, having large white

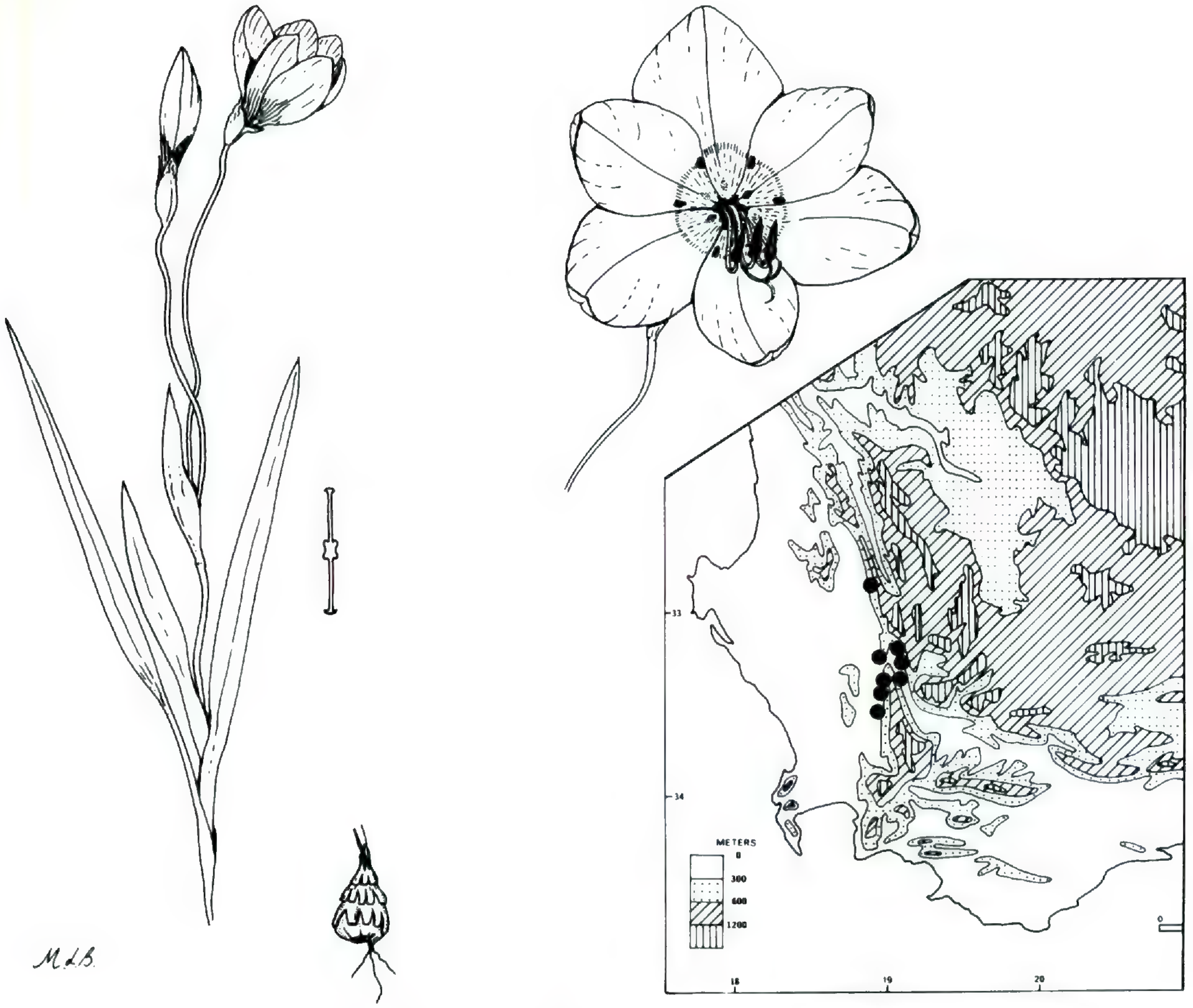


FIGURE 75. Morphology and distribution of *Geissorhiza tulbaghensis*. Habit and corm ×0.5; flower life size; leaf section enlarged (*Goldblatt 4755*, Tulbagh Cemetery).

flowers marked in the center with maroon-red to brown. It is fairly rare today, and its former range is becoming restricted to fewer sites as the fertile clay flats where it grows are planted to vines or cereals. It appears similar to the well known "wine cup," *G. radians*, and shares with it very similar floral morphology, having large zygomorphic flowers with declinate stamens and style. They are, however, unrelated, *G. tulbaghensis* having plane leaves and a puberulous stem typical of section *Planifolia* while *G. radians* has the linear, 2-grooved leaves and ribbed leaf sheaths characteristic of section *Geissorhiza*.

Geissorhiza tulbaghensis is distinctive not only in its flower coloration, but in its flat leaves which have a peculiar, slender petiole-like base, and puberulous stem. It is worth horticultural attention, and is easy to grow.

Loubser has recorded an interesting case of sympatry and hybridization involving *Geissorhiza tulbaghensis* on a farm NW of Porterville where this species occurs together with *G. inflexa* and *G. aspera*. Hybrids between both the latter and *G. tulbaghensis* are present and exhibit various degrees of intermediacy between the parents [*Loubser 2185, 2187, 2188* (BOL)].

Specimens examined. SOUTH AFRICA. CAPE: 3218 (Clanwilliam) Nurust farm, 8 mi. NW of Porterville (DD), *Loubser 2103* (NBG), *2190* (BOL).

3318 (Cape Town) Wellington (CB), *Dawson s.n* (BOL 14011), *Grant s.n.* (MO).

3319 (Worcester) Tulbagh (AC), *F. Bolus & L. Bolus s.n.* (BOL 14851, K, PRE), *Grant 2423* (MO, PRE), *Zeyher s.n.* (SAM 20866), *Stanford s.n.* (BOL); 2 mi. S of Tulbagh, *Lewis 5793* (NBG); Tulbagh Cemetery, *Goldblatt 4755* (K, MO, PRE, US), *5227* (K, MO, PRE); 3 mi. W of Tulbagh, *Marloth 7113* (PRE); Artois, S of Tulbagh, *H. Bolus s.n.* (BOL 7585); foot of Vogelvlei Mts., near Gouda, *Esterhuysen 18798* (BOL);

near Piketberg Road Station (Gouda), *Diels 1164* (B); Tulbagh turnoff, from Hermon, *Mauve 4645A* (PRE, STE).

WITHOUT PRECISE LOCALITY: Cape, *Boucher s.n.* (B "Herb. Lubeck").

SECTION *CILIATA*

12. Section Ciliata Goldbl., sect. nov. TYPE: *G. inflexa* (de la Roche) Ker.

Geissorhiza subsection *Pubescentes* Foster, Contr. Gray Herb. 135: 39. 1941. TYPE: *G. erosa* (Salisb.) Foster [= *G. inflexa* (de la Roche) Ker].

Tunicae cormi durae lignosae, foliis plerumque 3, ensiformibus ad linearibus marginibus costisque alatis ciliato-pubescentibus, caule glabro vel puberulo-ciliatis, bracteis infra herbaceis supra siccis ferrugineis, floribus actinomorphis stellatis, tubo brevi, staminibus aequalibus vel inaequalibus.

Corm tunics hard and woody, *leaves* with the margins and midrib moderately to strongly raised and winged, the midrib and sometimes other veins also winged, the edges ciliate-pubescent, ensiform to linear, *bracts* herbaceous below, dry and ferrugineous in the upper half, *flowers* stellate or hypocrateriform, actinomorphic, the tube short or reaching to the apex of the bracts, stamens equal or unequal .

Species. 10.

72. Geissorhiza namaquensis Barker, Fl. Pl. Africa 18: tab. 688. 1938; Foster, Contr. Gray Herb. 135: 51. 1941. TYPE: South Africa. Cape: Namaqualand, Klipfontein, *Phillips s.n.* (holotype, BOL 22163).

Plants (8–)12–30 cm high. *Corm* globose, 8–10 mm diam., somewhat asymmetric with one side obliquely flattened below and extended downward shortly, tunics dark brown, imbricate, notched below into more or less regular segments, and drawn into points above. *Leaves* usually 3, occasionally 4, about as long as the stem, 2–4 mm wide, evidently flat, but the margins raised and extending for a short distance at right angles to the blade and with ciliate edges, midrib also raised and winged and ciliate on the edges, sometimes a second pair of veins also ciliate, the lower two leaves basal, the third leaf inserted above the ground and sheathing below, similar but shorter than the basal leaves, fourth leaf, if present, shortest and becoming bract-like. *Stem* more or less erect, flexed at the base of the spike, minutely and sparsely puberulous below, sometimes with 1 branch. *Spike* inclined, flexed at the base, flexuose, 2–8-flowered; *bracts* green, herbaceous, dry and membranous, pale becoming brownish only near the apex, (9–)12–16(–20) mm long, the outer completely enclosing the smaller inner bract. *Flower* hypocrateriform, blue-purple; *perianth tube* (6–)8–11 mm long, reaching the apex of, or just exceeding the bracts, cylindric, widening near the throat; *tepals* 14–18 mm long, elliptic, to 4 mm wide. *Filaments* equal, 5–6 mm long; *anthers* (2–)4–6 mm long, yellow. *Ovary* 2–4 mm long, *style* dividing near the middle or towards the apex of the anthers, becoming unilateral, branches 1–3 mm long, recurved. *Capsule* globose, to 8 mm long. *Chromosome number,* unknown.

Flowering time. September to October.

Distribution. Northern Namaqualand, in Renosterbos type vegetation on shale and quartzite slopes. Figure 76.

Geissorhiza namaquensis and its more specialized, long-tubed relative, *G. kamiesmontana* are a closely related pair of species and the only members of the genus endemic in Namaqualand. Although at first glance *Geissorhiza namaquensis* resembles the Western Cape *G. aspera* (syn. *G. secunda* sensu auct.), its winged and ciliate leaf margins and midrib and its well-developed perianth tube suggest a very fundamental difference between them. *Geissorhiza namaquensis* and *C. kamiesmontana* are most likely related to species of section *Ciliata* where similar leaves are found. However, they seem taxonomically isolated in the section and probably represent a fairly old line, perhaps close to the ancestral type of the section, while the remaining species have evolved more rapidly and become specialized in their very short perianth tubes and dry bracts that are brown by the time the flowers open rather than drying after the flowers fade as in *G. namaquensis.*

Geissorhiza namaquensis occurs locally on the Kamiesberg on granitic soil, but elsewhere in Namaqualand is restricted to the few outcrops of shales and quartzites of the ancient Nama system, which once covered Namaqualand, but is now largely eroded away. All collections away from the Kamiesberg have been made in the north–south trending belt of Nama Shale that occurs west of Springbok and extends northward, somewhat beyond Steinkopf. This soil, very different from the granitic sands typical of Namaqualand, supports an interesting flora which shows many links with the Cape Flora to the

south (Goldblatt, 1979a: 388). It supports several Iridaceae either occurring elsewhere only in the Cape Region, or endemic, but having their closest affinities with Cape taxa.

Specimens examined. SOUTH AFRICA. CAPE: 2917 (Springbok) Klipfontein (B-), *Phillips s.n.* (Nat. Bot. Gard. 1471/30 in BOL, K); Steinkopf (BA), *Marloth 6782* (B, BOL, PRE, STE), *Herre s.n.* (STE 11844); stony hillside, Steinkopf, *Lewis 5495* (NBG); Kosies NW of Steinkopf, *van Berkel 399* (MO); Spektakel Pass W of Springbok (DA), *Goldblatt 2803* (K, MO, NBG, PRE, WAG); 15.25 mi. W by S of Springbok, renosterveld on shale and quartzite hills, *Acocks 19580* (K, M, NBG, PRE).

3018 (Kamiesberg) Leliefontein, foot of Kamiesberg Mt. (CC), *Le Roux & Ramsey 672* (PRE).

73. Geissorhiza kamiesmontana Goldbl., sp. nov. TYPE: South Africa. Cape: Kamiesberg, E slopes of Rooiberg near Welkom, *Goldblatt 5770* (holotype, MO; isotypes, K, NBG, PRE, WAG).

Planta (10–)15–30 cm alta, foliis 3–4, inferioribus duobus basalibus, marginibus elevatis, pubescentibus, costis centralibus elevatis alatis pubescentibus, caule pubescente, spicis florum 1–4, floribus hypocrateriformibus, atrocaeruleis, tubo 18–25 mm longo, tepalis 16–20 mm longis, stylo diviso prope basem antherarum.

Plants (10–)15–30 cm high. *Corm* globose, ca. 10 mm diam., somewhat asymmetric with one side flattened obliquely below and sometimes extending downward, tunics dark brown, imbricate, notched below into nearly regular segments and drawn into points above. *Cataphyll* 1 or 2, membranous, brownish. *Leaves* 3 or 4, ensiform, 2–3 mm wide, reaching to about the base of the spike, the margins lightly raised and extending at right angles to the blade, the midrib also raised and winged, the edges of the margins, midrib and other veins pubescent, the lower two leaves basal, the upper of these sheathing the stem shortly, the upper one or two cauline, the fourth leaf (when present) smallest and becoming bract-like. *Stem* erect, puberulent-pubescent throughout, including the spike axis, 1–2-branched. *Spike* 1–4-flowered; *bracts* green, becoming dry from the apex, eventually turning brown above, 12–18 (–21) mm long, the inner completely enclosed by the much longer outer bracts. *Flower* hypocrateriform, deep blue, with pale throat and tube; *perianth tube* 18–25 mm long, cylindric below, widening gradually above the bracts; *tepals* 16–20 mm long, elliptic, ca. 3 mm wide. *Filaments* 8–10 mm long, equal; *anthers* 3–4 mm long, yellow. *Ovary* ca. 3 mm long, *style* dividing near the base of the anthers, branches ca. 2.5 mm long, recurved, and reaching the middle of the anthers only. *Capsule* oblong to globose, 6–9 mm long. *Chromosome number*, $2n = 26$ (*Goldblatt 5770*).

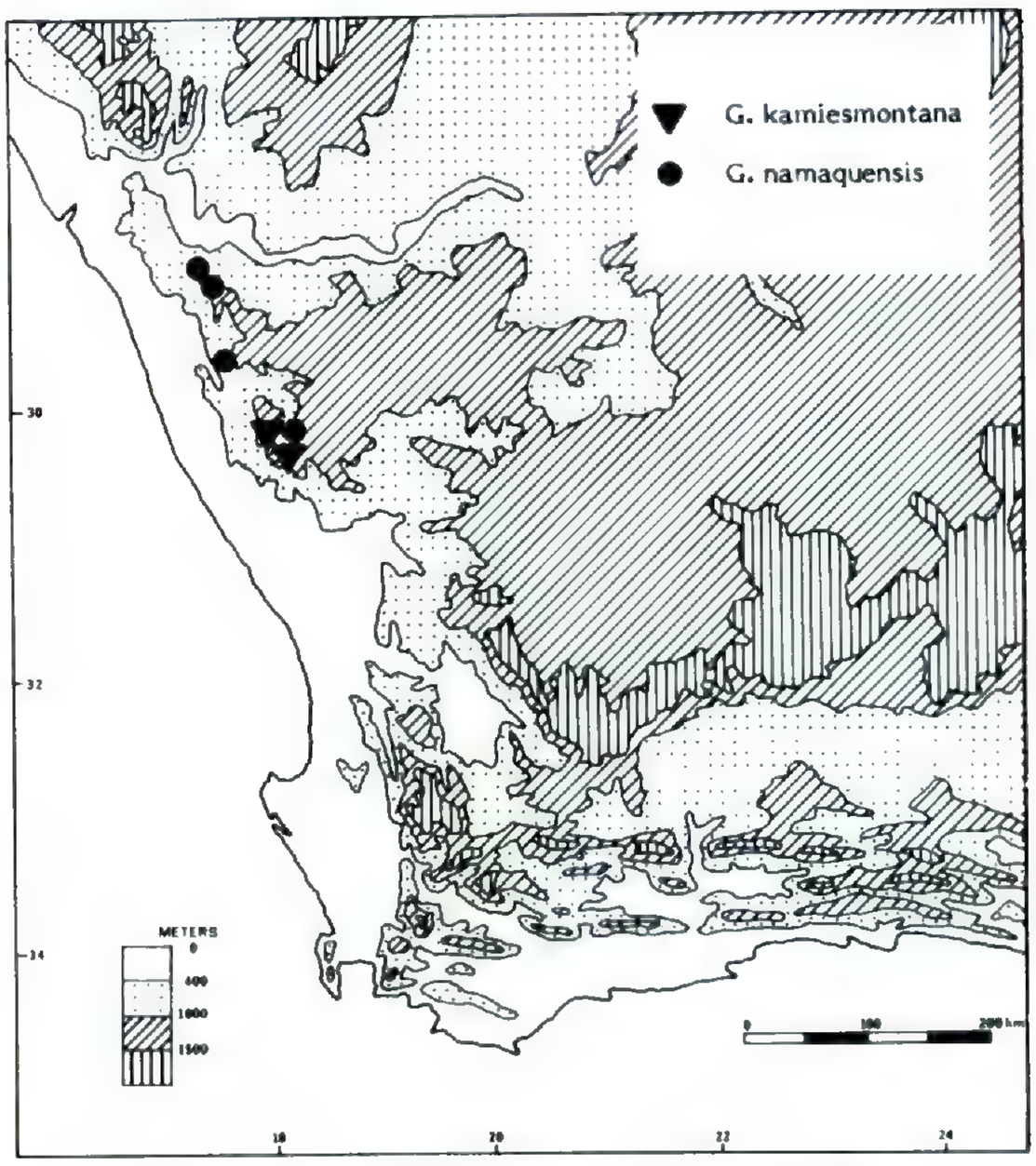


FIGURE 76. Distribution of *Geissorhiza namaquensis* and *G. kamiesmontana*.

Flowering time. September.

Distribution. Middle altitudes in the Kamiesberg, in central Namaqualand. Figure 76.

Geissorhiza kamiesmontana is known from only two gatherings from middle altitudes in the Kamiesberg Mountains of central Namaqualand, where it is apparently endemic and restricted to a few sheltered sites. I made the type gathering on the eastern slopes of the Rooiberg where shade from rocks and tall shrubs gave shelter to the plants which grow in shallow soil near seasonal pools and streamlets.

The species is clearly related to the other endemic Namaqualand species of *Geissorhiza*, *G. namaquensis* which is similar in general appearance. The two have identical corms, puberulent stems and similar leaves with raised and winged margins and pubescence on the margin and midrib edges. *Geissorhiza kamiesmontana* is easily distinguished from *G. namaquensis* by its well-developed perianth tube, 18–25 mm long which much exceeds the long bracts; its deep blue flower with a relatively short style, the branches of which do not exceed the anthers; and the heavy, almost

velvety, white pubescence on the leaves, stem, and inflorescence. The collection made by Leipoldt "in a kloof near Kamieskroon" has particularly long bracts (to 21 mm) compared with the type material, in which the bracts are to 18 mm long. The flowers of *Geissorhiza namaquana* are pale blue and have a much shorter tube, 6–11 mm long, which is usually about as long as the bracts, while the stem and leaf pubescence is less pronounced.

Specimens examined. SOUTH AFRICA. CAPE: 3017 (Hondeklipbaai) Kloof near Kamieskroon (BB), *Leipoldt 3815* (BOL).

3018 (Kamiesberg) E slopes of Rooiberg near Welkom (AC), *Goldblatt 5770* (K, MO, NBG, PRE, WAG), *6703* (MO).

74. Geissorhiza divaricata Goldbl., sp. nov. TYPE: South Africa. Cape: W of Nieuwoudtville, among rocks in fynbos, *Goldblatt 5838* (holotype, MO; isotypes, K, NBG). FIGURE 77.

Planta (15–)20–45 cm alta, foliis 3, duobus inferioribus basalibus erectis linearibus, marginibus extensis, floribus (2–)3–5, stellatis albis vel malvinescentibus, tubo 1–2 mm longo, tepalis ca. 10 mm longis, filamentis aequalibus, ca. 3 mm longis, antheris 3–4 mm longis, stylo diviso prope apicem antherarum, ramis recurvatis.

Plants (15–)20–45 cm high. *Corm* globose, tapering above, and obliquely flattened below, 10–12 mm diam., tunics blackish, imbricate notched below into segments. *Cataphyll* firm, brownish, persistent, and accumulating with leaf bases in a fibrous neck around the stem base. *Leaves* 3, linear to ensiform, 2–3 mm wide, the margins thickened and extending at right angles to the lamina, midrib extended and winged, and one or two pairs of veins enlarged, margin edges and veins ciliate-pubescent, the lower two leaves basal, half to about as long as stem, the uppermost leaf inserted in the middle part of the stem, sheathing the upper half of the stem for half to two-thirds its length. *Stem* erect, smooth, usually bearing in addition to the sheathing cauline leaf, one or more short, dry, membranous bracts, and branched from these nodes and also sometimes from the cauline leaf axil, sharply flexed above the nodes and at the base of the spike. *Spike* flexed at the base, inclined, (2–)3–5-flowered, flexuose; *bracts* dry, membranous and brown at flowering, flexed outwards in the upper half, 5.5–7 mm long, the inner shorter than the outer. *Flowers* stellate, white to pale mauve, reddish purple on the reverse of the outer tepals; *perianth tube* 1–2 mm long, much shorter than the bracts; *tepals* ca. 10 mm long, ovate-elliptic, ca. 4 mm wide. *Filaments* equal, ca. 3 mm long; *anthers* 3–4 mm long. *Ovary* 1–2 mm long, *style* dividing near the upper third of the anthers, branches recurved. *Capsule* globose, 4–5 mm long. *Chromosome number,* unknown.

Flowering time. September.

Distribution. Nieuwoudtville Escarpment and Gifberg, in rocky situations in fynbos. Figure 77.

Geissorhiza divaricata is apparently very closely allied to *G. subrigida,* a poorly known species of the Nieuwoudtville area. The two are distinctive in having a sheath of fibers around the stem base, smooth stems, ciliate to pubescent and ribbed leaves, divaricate branching, and brown, membranous stem bracts. These shared similarities have tended to obscure their differences and *G. divaricata* has until now been identified with *G. subrigida.* The differences between the two species, however, seem significant. *Geissorhiza divaricata* has small white to pale mauve flowers with a perianth tube 1–2 mm long and tepals ca. 10 mm, while *G. subrigida* has large blue to violet flowers with perianth tube 3–4 mm long and tepals 12–17 mm long. Also *G. divaricata* tends to be taller and more branched and it has smaller corms than the shorter and few branched *G. subrigida.* Both grow along the Nieuwoudtville Escarpment in the rocky sandstone soils of the area, but have not been recorded growing together. The Nieuwoudtville area is a well known center of endemism for geophytic plants, Iridaceae in particular, so the occurrence of two distinct, but closely allied species here is not particularly surprising.

Included in *Geissorhiza divaricata* are two collections from the Gifberg, a short distance to the southwest, *Barker 9571* and *Bayliss 6187,* specimens of which have either simple or single branched stems and lack the distinctive dry stem bracts found in the Nieuwoudtville populations. The specimens approach *Geissorhiza erubescens* in outward appearance, but do not have the pubescent stems of that species.

Specimens examined. SOUTH AFRICA. CAPE: 3118 (Vanrhynsdorp) top of Gifberg Pass (DD), *Barker 9571* (NBG), *Bayliss 6187* (MO).

3119 (Calvinia) near Nieuwoudtville (AC), *Leipoldt 821* (BOL, SAM), *L. Bolus s.n.* (BOL 21060); fynbos W of Nieuwoudtville in rock crevices, *Goldblatt 5838* (K, MO, NBG); Uitkomst farm, SW of Nieuwoudtville, *Barker 10745* (K, NBG).

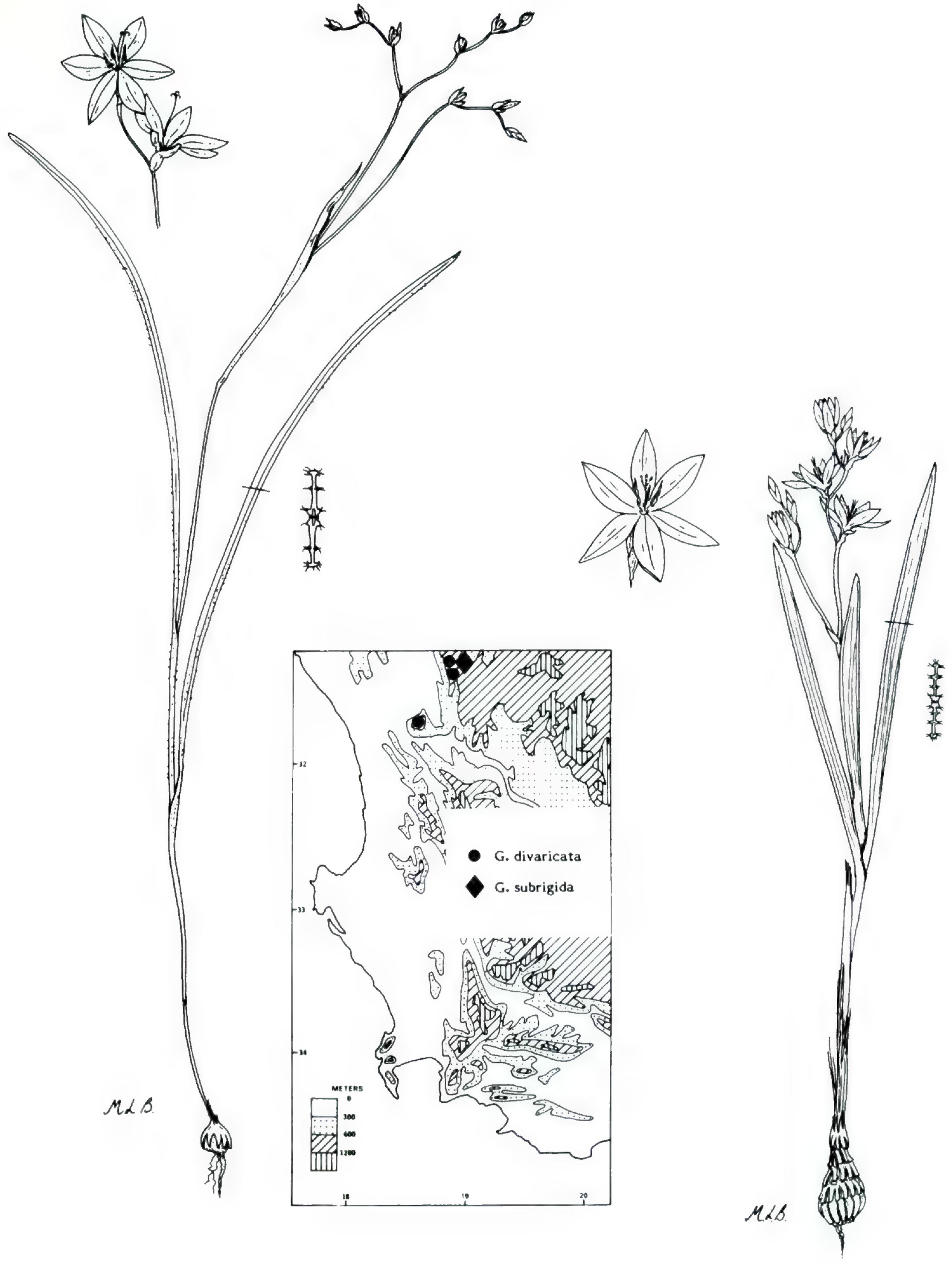


FIGURE 77. Morphology and distribution of *Geissorhiza divaricata* (left) and *G. subrigida* (right). Habits ×0.5; flowers life size; leaf sections much enlarged (*G. divaricata, Goldblatt 5838,* Nieuwoudtville Escarpment; *G. subrigida, Goldblatt 7220,* W of Nieuwoudtville).

75. Geissorhiza subrigida L. Bolus, S. African Gard. 22: 275. 1932. TYPE: South Africa. Cape: near Nieuwoudtville, cult. in hort. L. Bolus, Cape Town, *Buhr s.n.* [holotype, BOL 19995 (publ. as 19943); isotypes, K, PRE]. FIGURE 77.

Plants 12–20(–30) cm high. *Corm* globose, tapering above, and obliquely flattened below, 1–1.5 cm diam., tunics blackish, imbricate, notched below into segments. *Cataphyll* firm, brownish, persistent and accumulating with leaf bases in a fibrous neck around the stem base. *Leaves* 3, half to about as long as the stem, 3–6 mm wide, the margins thickened and extending at right angles to the blade, the midrib also raised and winged and at least two other pairs of veins enlarged, ciliate to pubescent on the veins and margin edges, the lower two leaves basal, the uppermost inserted in the middle part of the stem and sheathing for at least two-thirds its length, several ribbed. *Stem* erect, smooth, bearing in addition to the sheathing cauline leaf, a short, dry, membranous bract and usually branched from this node and also sometimes from the axil of the cauline leaf, flexed above the nodes and at the base of the spike. *Spike* flexed at base, (2–)3–5-flowered, flexuose; *bracts* 6–10 mm long, dry, membranous and brown at flowering time, flexed outward in the upper half, the inner shorter than the outer. *Flowers* stellate, violet blue, pale in the tube; *perianth tube* 2–3 mm long, shorter than the bracts; *tepals* 12–17 mm long, ovate-elliptic, to 7 mm wide. *Filaments* equal, ca. 4 mm long; *anthers* 4–5 mm long. *Ovary* 1.3–2 mm long, *style* dividing at or near the apex of the anthers, becoming declinate, branches recurved. *Capsule* globose, ca. 4 mm long. *Chromosome number,* unknown.

Flowering time. August to mid-September.

Distribution. Sandy soils around Nieuwoudtville. Figure 77.

Geissorhiza subrigida is an unusual species with comparatively large blue to violet flowers, strongly ciliate-pubescent leaves and a divaricate branching pattern. It is very local in distribution, being recorded only from the immediate vicinity of the town of Nieuwoudtville in the northwestern Cape. Closely allied is *G. divaricata* which is similar in vegetative morphology, but has smaller, white to pale mauve flowers. The similarities and differences between these two species are discussed more fully following the description of *G. divaricata.*

The leaves of *Geissorhiza subrigida* and *G. divaricata,* with their raised and flattened margins extending at right angles to the lamina and the raised and winged midrib, both ciliate on their edges are similar to those of *G. inflexa* and *G. heterostyla* in particular, although the latter two have a lighter pubescence. They seem well placed in section *Ciliata,* in which their branched habit, the presence of stem bracts, and their equal stamens suggest that they are fairly unspecialized.

Specimens examined. SOUTH AFRICA. CAPE: 3119 (Calvinia) Nieuwoudtville (AC), *Buhr s.n.* (cult.) (BOL 19995, K, NBG 60617, 60618, PRE, STE 17319); Glenridge farm, Nieuwoudtville, *Lewis 5886* (NBG); shallow sandy soil in recently burned veld W of Nieuwoudtville, S of the old road to the pass, *Goldblatt 7220* (K, MO, PRE).

76. Geissorhiza heterostyla L. Bolus, S. African Gard. 20: 345-346. 1930; Foster, Contr. Gray Herb. 135: 44–45. 1941. TYPE: South Africa. Cape: near Whitehill, *L. Bolus s.n.* (lectotype, BOL 19148, here designated; isolectotypes, BM, BOL, K). FIGURE 78.

Gessorhiza rogersii N. E. Br., Kew Bull. 452. 1931. TYPE: South Africa. Cape: Worcester, between Osplaats and Tunnel Sidings, 600–900 m, *Rogers 16725* (lectotype, K, here designated; isolectotypes, J, K).

Hesperantha rosea Klatt, Abh. Naturf. Ges. Halle 15: 395 (Erg. 61). 1882. TYPE: South Africa. Cape: Knysna, *Newdegate s.n.* (holotype, B "Herb. Lubeck").

Geissorhiza rosea (Klatt) Foster, Contr. Gray Herb. 135: 48. 1941, hom. illeg. non Ecklon, Topogr. Verz. Pflanzensamml. Ecklon 20. 1827 [= *G. inflexa* (de la Roche) Ker].

Hesperantha ciliata E. Mey. ex Klatt, Abh. Naturf. Ges. Halle 12: 394 (Erg. 60). 1882. TYPE: South Africa. Cape: Hexriverskloof, *Drège s.n.* (holotype, B "Herb. Lubeck"), nom. superfl. pro *Geissorhiza rosea* Ecklon.

Plants 12–45 cm high. *Corm* symmetric, 4–12(–15) mm diam., globose, tunics blackish, woody, outer accumulating above, and notched regularly into segments below. *Cataphyll* membranous, often dark above. *Leaves* 3, linear to ensiform, 2–5 mm wide, half to about as long as the stem, the margins raised and extended at right angles to angles to the blade and ciliate on the edges, the midrib also raised and ciliate, the lower two leaves basal, the uppermost basal or cauline, sheathing for most of its length, several

ribbed on the sheath. *Stem* erect, puberulous to ciliate or smooth, simple or more often branched, sheathed for up to three-fourths its length, bearing a membranous, often dry, bract leaf in the upper part, and usually branching from this axil, or also from the axil of the sheathing leaf. *Spike* (1–)2–7-flowered, flexed at base and flexuose; *bracts* 7–10(–15) mm long, initially pale green with hyaline margins, but drying from apex and becoming transparent, or flushed red or brown, the inner shorter than the outer. *Flower* stellate, either white, flushed pink to purple on reverse of the tepals, or pale blue to mauve, white to yellow or occasionally dark purple in the throat; *perianth tube* 1–2 mm long; *tepals* 10–18(–22) mm long, obovate, 6–9 mm wide. *Filaments* unequal, the two longer 4–6 mm long, the shorter 3–4 mm long; *anthers* (2.5–)4–6 mm long, yellow or blue-black. *Ovary* 1.5–3(–4) mm long, *style* short to long, either dividing near the base of filaments, with long branches, or reaching to the base or to the apex of the anthers and branches short or long, ultimately recurved. *Capsule* globose, 5–8 mm long. *Chromosome number*, $2n = 26$ (*Hall 193*—as *Hall s.n.*, Voelvlei, Sutherland; *Goldblatt 135*—as *G. leipoldtii, 5815, 6265*), 26 + 2B (*Goldblatt 5211*).

Flowering time. August to early October.

Distribution. Widespread from the Kubiskouw Mountains in south Namaqualand through the Roggeveld and Witteberg to the southern Cape as far east as Port Elizabeth; on various soils but usually on sand in the Cape Floristic Region. Figure 78.

Geissorhiza heterostyla was described by H. M. L. Bolus in 1930 based on a collection of plants from Whitehill in the western Karoo. The outstanding characteristic of the type collection is the variable length of the style. Plants have either long styles, dividing beyond the apex of the anthers; medium styles dividing at anther level; or short styles, dividing below anther level. Other distinguishing features of the collection are a puberulous stem; a submembranous stem bract; leaves with winged, ciliate margins; and unequal stamens, the latter feature not noticed by Bolus, but quite evident in the ample type material.

Other collections matching the type have since been made in the same area, e.g., *Lewis 4790*—Eendracht; *Barker 7492*—Tweedside; *Compton 3772*—Cobita—all heterostylous, as well as a few like *Compton 15172* and *Leighton 201*, both from the nearby Witteberg that cannot be distinguished from *G. heterostyla* except that the styles are invariably long. *Phillips 1549*, from Seven Weeks Poort, consists of heterostylous plants with either smooth or sparsely papillose stems. The nonheterostylous collections from the Witteberg match closely plants from the Ceres, Koo, and Hex River Valleys, e.g., *Esterhuysen 20344*—Eselsfontein; *Barker 1473*—Theronsberg; *Loubser 2061*—Koo Valley; *Oliver 5015*—Prince Alfreds Hamlet; and *Rogers 16725*—Osplaats—Tunnel Sidings, the latter the type collection of *G. rogersii* (Brown, 1931).

Heterostylous gatherings of *Geissorhiza heterostyla* have also been made in the Roggeveld, in the Calvinia district, and in the Kubiskouw Mountains in southern Namaqualand. Again, some collections that match the heterostylous material appear to consist solely of long-styled plants (*Goldblatt 549*—Verlaten Kloof; *Goldblatt 5815*—near Middelpos; *Goldblatt 5824*—Hantamsberg). It is clear that the homostylous populations are the same taxon, and *G. heterostyla* must now be regarded as consisting of either heterostylous or homostylous populations. *Geissorhiza rogersii* accordingly falls into synonymy of *G. heterostyla*.

The Witteberg, Ceres, and Hex River Valley populations of *G. heterostyla* are generally smaller, and less robust than plants from the Roggeveld and the Calvinia district (though not invariably), and in turn are easily confused with plants named *G. rosea* (Klatt) Foster (actually a homonym for *G. rosea* Ecklon), which can be separated by their having leaves with less strongly elevated margins and usually smooth stems. Populations of plants matching *G. rosea* sensu Foster extend from Worcester south and east along the Langeberg and southern coast to Port Elizabeth, usually occurring on sandy soils. Plants are not always slender or invariably with smooth stems. Some notable exceptions are *Goldblatt 2544*—Op de Tradouw, robust and with puberulous stems; *Goldblatt 4929*—Humansdorp, also very robust; *Beacom s.n.*—near Joubertina, slender but with a puberulous stem; and *Esterhuysen 24654*—foot of Leeuriviersberg, slender to fairly robust plants with a puberulous stem.

Plants that would be considered to be *Geissorhiza rosea* grade into the homostylous form of *G. heterostyla* to the extent that it seems unreasonable to maintain them as a distinct species. Nor is there any good character except perhaps

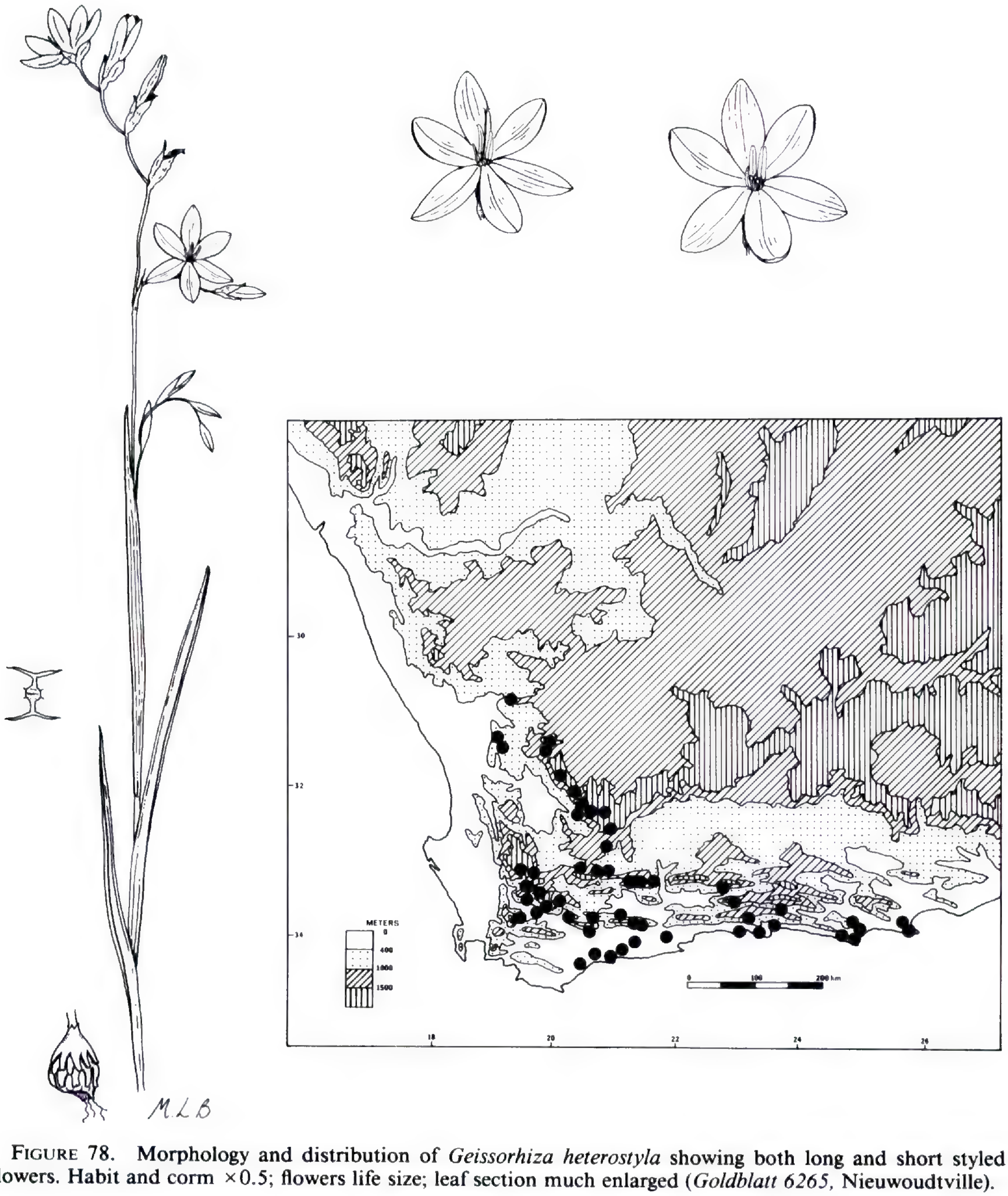


FIGURE 78. Morphology and distribution of *Geissorhiza heterostyla* showing both long and short styled flowers. Habit and corm ×0.5; flowers life size; leaf section much enlarged (*Goldblatt 6265*, Nieuwoudtville).

the degree of leaf margin elevation that can be consistently used to separate them. Thus *G. rosea* and its synonyms *Hesperantha ciliata* E. Mey. ex Klatt nom. superfl. and *G. ciliaris* Salisb. are here regarded as conspecific with *G. heterostyla*. While there may be some merit in establishing a subspecific taxonomy for *G. heterostyla* it seems quite arbitrary to which subspecific taxa some of the intermediate forms should be assigned. I have decided therefore, not to formally recognize subspecific taxa. Those who need to refer to one of the forms of *G. heterostyla* should use an informal trinomial terminology as suggested by Burtt (1970). Thus slender and smooth (rarely puberulous) stemmed and long-styled plants with leaf margins raised relatively little compared to leaf width can be referred to as *G. heterostyla* (*rosea*). Populations of heterostylous plants, typically with puberulous stems (rarely smooth) and leaves with margins raised well above the leaf surface can

similarly be designated *G. heterostyla* (*heterostyla*), while homostylous populations can be designated *G. heterostyla* (*rogersii*).

Two more forms of *Geissorhiza heterostyla* need to be mentioned. The first consists of distinctive plants with medium to large white flowers (*Thomas s.n.*—Eilandia Road; *Olivier 283*—Karoo Garden) which initially appears different from other populations. Little more than a color difference however seems to be involved, as similarly large-flowered plants occur elsewhere. The second population, from Stettynskloof, south of Worcester (*Barker 9455*), incidentally the most westerly station, seems fairly typical at first having very unequal stamens and pale flowers. All but one of the several specimens on the sheet lack the membranous stem bract, and except for the unequal stamens these plants are very like the related *G. inflexa* which occurs in this area and to the south. It seems that this population, on the edge of the range of *G. heterostyla,* is intermediate in some respects with *G. inflexa,* possibly as a result of introgressive hybridization.

Some collections from the Sutherland district, notably *Hanekom 1562*—Houthoek and *Acocks 15963*—Klipbanksrivier, are remarkably robust and the large flowers are purple with darker pigmentation in the center. These specimens appear to represent a distinct local race or form of *G. heterostyla*.

Specimens examined. SOUTH AFRICA. CAPE: 3019 (Loeriesfontein) Kubiskouw, near summit (CD), *Marloth 12870* (PRE).

3119 (Calvinia) near Nieuwoudtville on the Loeriesfontein road (AC), *Lewis 5850* (NBG); 1 mi. N of Nieuwoudtville, *Barker 9563* (NBG, S, STE), *Goldblatt 135* (J); Grasberg road NW of Nieuwoudtville, *Goldblatt 6265* (MO); W end of the Hantamsberg Plateau (BC), *Goldblatt 5824* (K, MO, NBG); upper slopes below cliffs at the W end of the Hantamsberg, *Goldblatt 5805* (K, MO, NBG, PRE); wet red clay, top of Hantamsberg (BD), *Goldblatt 426* (BOL); Driefontein voor Hantam (DA), *Marloth 12811* (PRE).

3120 (Williston) Blomfontein farm, E of Middelpos (CC), *Barker 10774* (K, NBG); 66 km S of Calvinia, on road to Blomfontein, *Goldblatt 5815* (MO, PRE);

3220 (Sutherland) Geelhoek (Vyffontein), Sutherland (AB), *Acocks 17175* (PRE); Quaggasfontein, NW of Sutherland, *Goldblatt 6355* (MO); Houdenbek, NW of Sutherland (AD), *Thompson 1796* (K, STE); Voelfontein, S of farm house, *Goldblatt 6322* (MO); Voelfontein, *Hall 193* (NBG, S); Jakhals Valley, Sutherland (BC), *Marloth 9654* (PRE); top of Verlaten Kloof, *Goldblatt 549* (BOL); Houthoek, Sutherland (CA), *Hanekom 1562* (MO, NBG, PRE); Klipbanksrivier, foot of the Roggeveld Mts. (CB), *Acocks 16963* (K, PRE); 13.5 mi. SSW of the foot of Komsberg Pass (DC), *Acocks 18447* (BOL, K, PRE); 20 mi. SSW of the foot of Komsberg Pass, *Leistner 269* (PRE).

3319 (Worcester) Gydo Pass, lower slopes (AD), *Hafstrom & Acocks 284* (K, PRE); flats NW of Prince Alfreds Hamlet, *Oliver 5015* (PRE); Eselsfontein, Ceres, *Esterhuysen 20344* (BOL); Ceres, *Lindeberg s.n.* (S), *Rogers 28701* (Z); Hex River Valley (BC-DA), *Tyson 723* (SAM); Theronsberg, Ceres (BC), *Barker 1473* (NBG); Prospect Peak, Hex River Mts., SE slopes (BC), *Esterhuysen 15941* (BOL); Onse Rug farm (CB), *Barker 9443* (NBG); lower slopes of Fonteintjiesberg, Onse Rug farm, *Goldblatt 4089* (E, MO, PRE, S, US, WAG); Worcester, Nature Reserve, *Olivier 283* (K); Stettynskloof (CD), *Barker 9455* (NBG); Eilandia road, 5–6 mi. from Worcester-Robertson road (DA), *Thomas s.n.* (NBG 93061, PRE 58032); NW entrance to Koo valley (DB), *Loubser 2061* (NBG); Langeberg, above Berg-en-Dal, cliff face, 2,200 ft., *Esterhuysen 35684* (BOL, MO); Berg-en-Dal, above Klaasvoogds, slopes near the base of the Langeberg, *Esterhuysen 35797* (MO, PRE, WAG).

3320 (Montagu) Voetpadsberg, Tweedside (AB), *Barker 7492* (NBG); Tweedside, *Lewis s.n.* (Nat. Bot. Gard. 2694/32 in BOL, K, SAM); Witteberg, Laingsburg (BA), *Leighton 201* (BOL); Witteberg at Bantams, 5,000 ft., *Compton 12244* (NBG); Witteberg, Whitehill, *Compton 13997* (NBG), *15172* (NBG), *16277* (NBG); Whitehill, *L. Bolus s.n.* (BM, BOL 19148); Donkerkloof, Montagu (CC), *Lewis 4789* (SAM); slopes at foot of the Langeberg near Leeuriviersberg (CD), *Esterhuysen 24564* (BOL, PRE); Op-de-Tradouw, W of Barrydale (CD), *Goldblatt 2844* (MO, PRE).

3321 (Ladismith) Elandsberg (Torenberg), Klein Swartberg, Ladismith, 3,000 ft. (AD), *Wurts 1174* (NBG); Seven Weeks Poort, *Phillips 1549* (SAM); Ladismith, *Loubser 2086* (NBG); Gamka Nature Reserve, Calitzdorp (BC), *Vlok 316* (MO, SAAS); The Oaks, Gysmanshoek Pass, Riversdale (CC), *van Wyk 722* (MO, STE); damp slope, Garcias Pass, *Lewis 5646* (NBG).

3322 (Oudtshoorn) Swartberg, hills above the Cango Caves (AD), *Vlok 292* (MO, NBG, SAAS); Kammanassie Mts., 2,800 ft. (DB), *Viviers & Vlok s.n.* (MO, SAAS).

3323 (Willowmore) Bo Koega, near Joubertina, *Bayliss 5954* (MO); hills N of Kruisfontein (CC), *Fourcade 4430* (STE); Joubertina, beside National Road (DD), *Beacom s.n.* (NBG 87524, 92829).

3324 (Steytlerville) 4 mi. N of Humansdorp, Hankey road (DD), *Fourcade 6160* (STE).

3420 (Bredasdorp) Swellendam (AB), *Fry sub Galpin s.n.* (B); Limestone hills, De Hoop (AD), *Lewis 6019* (M, NBG); Potteberg, ledges on S slopes (BC), *Esterhuysen 23210* (BOL, K); Hamerkop, S side of Potteberg, *Acocks 22745* (PRE); valley behind Oyster Beds Hotel, Fort Beaufort (BD), *Marsh 824* (K, STE); Cape Infanta, *Blum 18* (E); Duiwenhokrivier Kloof, between Port Beaufort and Riversdale, *Lewis 6013* (MO, NBG, STE).

3421 (Riversdale) Still Bay, ridge below the reservoir (AD), *Bohnen 4251* (STE); Roodehoogte, near Herbertsdale (BB), *Muir 1271* (BOL); Langeberg foothills N of Herbertsdale, *Goldblatt 4156* (MO, PRE, S).

3423 (Knysna) Victoria Bay, George (AA), *Barker 8181* (NBG, STE); slopes above Victoria Bay, *Lewis 3631* (SAM); near George, *Burchell 6088* (K); Noetzie

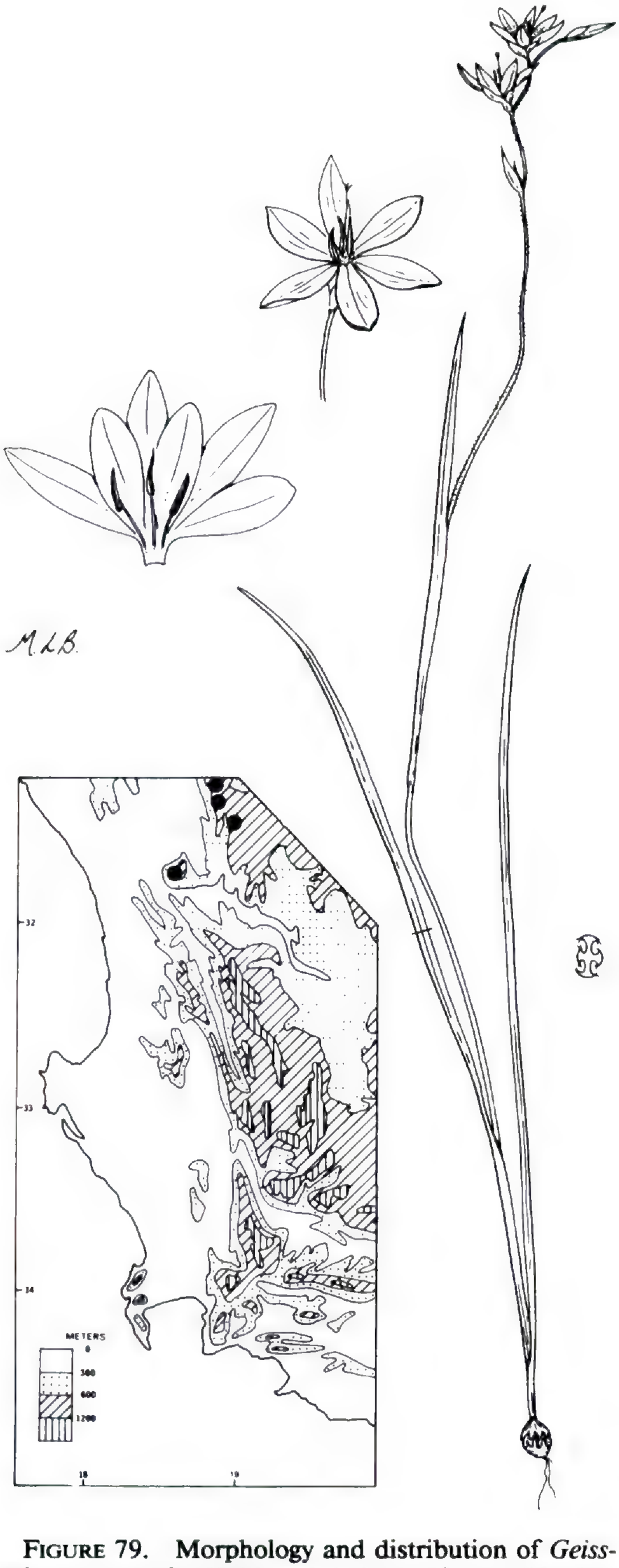


FIGURE 79. Morphology and distribution of *Geissorhiza arenicola*. Habit ×0.5; intact flower life size; opened flower ×1.5; leaf section much enlarged (*Goldblatt 7056*, heathland W of Nieuwoudtville).

(BA), *Middlemost s.n.* (NBG 60637, SAM 61725); national road outside Plettenberg Bay (AB), *Goldblatt 2912* (MO, WAG); Keurbooms River, *Galpin 4681* (K, PRE); Plettenberg Bay, *Fourcade 4806* (BOL, MO, STE), *Salter 6941* (BOL).

3424 (Humansdorp) Oudebos flats (AA), *Fourcade 967* (BOL), *3364* (BOL, K, PRE, STE); Krom River, W of Humansdorp (BA), *Acocks 21476* (PRE); duine veld, E of Kromme River mouth (BB), *Fourcade 2781* (STE); 4 km E of Humansdorp, *Goldblatt 4929* (MO), *5211* (MO, PRE); 8.5 mi. E of Humansdorp on road to Cape St. Francis, *Thompson 901* (STE); near Humansdorp, *Tyson 3067* (K, SAM, Z), *Barker 9068* (NBG), *Thode A1038* (PRE), *Galpin 4671* (K, PRE).

3425 (Port Elizabeth) Patons farm, Baakens River (DC), *Long 470* (K, PRE); Port Elizabeth, *Paterson 762* (BOL, PRE), *Fries, Norlindh & Weimarck 217* (K, LD, PRE, SAM); Baakens River, *Long 441* (K, PRE).

WITHOUT PRECISE LOCALITY: Riversdale (? dist.), *Rust 13* (B), *55* (B); Cape of Good Hope (C.B.S.), *Sparrman s.n.* (S), *Bowie 18* (BM).

77. Geissorhiza arenicola Goldbl., sp. nov. TYPE: South Africa. Cape: sandy wet heathland west of Nieuwoudtville, *Goldblatt 7056* (holotype, MO; isotypes, K, NBG, PRE, S). FIGURE 79.

Planta 12–26 cm alta, tunicis cormi imbricatis duris, foliis 3, inferioribus duobus basalis linearibus, superiore caulem infra vaginante, caule erecto, pubescenti supra, saepe infra glabro, spica (1–)3–8 florum, floribus stellatis, albis vel caeruleo-malvinis, tubo 1.5–2 mm longo, tepalis 10–15 mm longis, filamentis inaequalibus, antheris 3–5 mm longis, stylo diviso prope apicem antherarum.

Plants 12–26 cm high. *Corm* globose, 6–10 mm diam., symmetric, tunics blackish, imbricate, woody, notched into regular segments below. *Cataphyll* solitary, membranous. *Leaves* 3, narrow, linear, 1–2 mm wide, reaching the midline of the stem or the base of the spike, the margins and midrib enlarged and thus 2-grooved on each surface, the edges of the margins and midrib minutely ciliate or evidently smooth, often sticky below and with adhering sand, the lower two leaves basal, the uppermost inserted shortly above ground, often largest, sheathing the stem for two-thirds of its length, the sheath several ribbed and somewhat inflated. *Stem* erect, puberulent above the third leaf, smooth below, occasionally with 1 branch, without a sheathing bract. *Spike* flexuose, inclined, (1–)3–8-flowered; *bracts* herbaceous, the margins often lined with red above, sometimes becoming dry and membranous from the apex, 7–9 mm long, the inner shorter and much narrower than the outer. *Flower* stellate, white or deep blue-mauve and then pale in the throat; *perianth tube* 1.5–2 mm long, enclosed in the bracts, infundibuliform; *tepals* 10–15 mm long, 4–8 mm wide, oval. *Filaments* slightly unequal, 3–4 mm long, one 1–1.5 mm shorter than the other two; *anthers* 3–5 mm long, pale yellow. *Ovary* 1.5–2 mm long, *style* dividing at the apex of the anthers, branches ca. 2 mm

long, recurved. *Capsule* unknown. *Chromosome number,* $2n = 26$ (*Goldblatt 7056*).

Flowering time. September to mid-October.

Distribution. Nieuwoudtville Escarpment, between Grasberg and Lokenberg, and on the Gifberg, in stony Cape mountain soil. Figure 79.

Geissorhiza arenicola is endemic to the Gifberg and Nieuwoudtville Escarpments where it grows in the rocky, poor sandstone-derived soil typical of the mountains of the Cape System. It is nowhere common, but has been collected at four places along the Nieuwoudtville Escarpment as well as on the Gifberg a short distance to the southwest. *Geissorhiza arenicola* is distinctive in its puberulent stem; heavily ribbed and grooved upper leaf sheath; sticky basal leaves with strongly raised margins; and slightly to distinctly unequal stamens. While blue is the usual flower color, the collection from Lokenberg, *Acocks 17251,* is described as having white flowers.

It is apparently related to the better known and striking, brilliant blue-flowered *Geissorhiza splendidissima* with which it shares several important features, including a puberulent stem; a strongly ribbed and grooved upper leaf sheath; short perianth tube; and basal leaves with strongly raised margins and midrib, the edges of which are usually lightly ciliate. These two species have been assigned to section *Ciliata,* but as discussed under *G. splendidissima,* they are exceptional in this alliance in their strongly ribbed upper leaf sheath, a characteristic of section *Geissorhiza. Geissorhiza arenicola* shows some resemblance to the Nieuwoudtville endemic, *G. sulphurascens,* a species which has creamy yellow flowers and a smooth stem. The similarity is probably coincidental, and the two species can always be distinguished by several different characters.

Specimens examined. SOUTH AFRICA. CAPE: 3118 (Vanrhynsdorp) Gifberg (DC), *Phillips 7518* (NBG, PRE, STE).

3119 (Calvinia) Nieuwoudtville Escarpment in fynbos W of town, 3 km S of the Calvinia road (AC), *Goldblatt 5837* (MO); 5 mi. NW of Nieuwoudtville on Grasberg road, *Barker 9560* (M, NBG); wet sandy heathland W of Nieuwoudtville, *Goldblatt 7056* (K, MO, NBG, PRE, S); wet sandy meadows, Bokkeveld, *Marloth 7641* (PRE); Lokenberg, arid fynbos (CA), *Acocks 17251* (PRE).

FIGURE 80. Morphology and distribution of *Geissorhiza splendidissima.* Habit × 0.5; flower life size; leaf section much enlarged (*Goldblatt s.n.,* Glenlyon farm, Nieuwoudtville).

78. Geissorhiza splendidissima Diels, Bot. Jahrb. Syst. 44: 117. 1909; Foster, Contr. Gray Herb. 135: 31. 1941. TYPE: South Africa. Cape: Oorlogskloof, *Diels 627* (holotype, B). FIGURES 12, 80.

Plants 8–20 cm high. *Corm* ovoid, truncate at base, 7–10 mm diam., tunics dark, imbricate, the outer layers incised below into regular truncate segments. *Cataphyll* not evident. *Leaves* 3, linear, shorter to slightly longer than the stem, (1–)1.5–2 mm wide, the margins raised and extending at right angles to the blade, the midrib thickened, the blade thus narrowly 2-grooved on each surface, the edges of the margins and the midrib minutely ciliate, slightly sticky and with sand adhering in places, the lower two leaves basal, the lowermost longest, the uppermost inserted shortly above the ground, sheathing the stem below, wider than the basal leaves, the sheath somewhat inflated. *Stem* erect, densely and minutely puberulent, sheathed below and with a short bract leaf above, simple or with a single, or rarely 2 branches. *Spike* (1–)2–5(–6)-

flowered, flexed at the base of the spike; *bracts* green, becoming dry and brown from the apex, the outer 16–20(–25) mm long, the inner 8–16 mm long. *Flower* deep blue-violet, darker towards the base of the tepals, and yellowish in the throat, tepals cupped, zygomorphic, the stamens unilateral and declinate, held above the dorsal tepal; *perianth tube* 2–4 mm long, widening from the base; *tepals* broadly ovate, 15–22 mm long, outer 9–14 mm wide, inner 8–12 mm. *Filaments* ca. 5 mm long, equal, unilateral and declinate; *anthers* unilateral, horizontal, lying over the dorsal tepal, 7–8 mm long, pollen red-brown. *Ovary* ca. 3 mm long, *style* 10–11 mm long, lying below the stamens, dividing at the apex of the anthers, branches 2 mm long, recurved. *Capsule* globose, 6–7 mm long, to 5 mm diam., enclosed in the bracts. *Chromosome number,* $2n = 26$ (*Goldblatt 347*).

Flowering time. Late August to September.

Distribution. Sandy to stony flats to the north and south of Nieuwoudtville, east of the escarpment above Van Rhyns Pass. Figure 80.

Geissorhiza splendidissima is endemic to the area immediately around Nieuwoudtville in the northwestern Cape, where it grows in light clay soil among low-growing shrubs. It flowers well only when the surrounding vegetation has been cleared or disturbed and then it may make a striking display. The large, glossy deep blue-violet flowers are amongst the most beautiful in the genus and the species is well worth horticultural attention.

The affinities of *Geissorhiza splendidissima* seem to be with section *Ciliata,* the species of which have similar leaf morphology, with strongly raised margins and winged margins that are ciliate on the edges. Its puberulent stem is also consistent with this disposition for several species of the section also have this feature. The zygomorphic flowers of *G. splendidissima* are unique in the section and must be regarded as having evolved independently in this species and not indicative of a relationship to other sections in which there are species with similar zygomorphic flowers. It is somewhat unusual in section *Ciliata* also in the somewhat ribbed sheath of the uppermost leaf. This character is shared with the apparently allied *G. arenicola* and this seems to set these two species somewhat apart in the section.

Specimens examined. SOUTH AFRICA. CAPE: 3119 (Calvinia) Nieuwoudtville-Grasberg road (AC), *Goldblatt 347* (BOL); ca. 1 mi. N of Nieuwoudtville, *L. Bolus s.n.* (BM, BOL 19439, K); Nieuwoudtville, *Salter 1645* (BM), *Buhr s.n.* (Nat. Bot. Gard. 636/29 in BOL, Nat. Bot. Gard. 300/37, 299/39 in NBG, 822/30 in K); cult. in hort. Martley, Banhoek, ex Nieuwoudtville, *Buhr s.n.* (BOL), *Loubser 945* (NBG); Grasberg, 15 mi. NW of Nieuwoudtville, *Barker 9549* (NBG, UC); Charlies Hoek, *Barker 10759* (NBG); between Oorlogskloof and Papkuilsfontein, *Leipoldt 3035* (BOL, PRE); Willemsrivier, Calvinia, *Leipoldt 817* (SAM); Bokkeveld, Oorlogskloof, *Diels 627* (B); Glenlyon farm, Nieuwoudtville, *Hardy 67* (G, K, PRE, Z).

79. Geissorhiza inflexa (de la Roche) Ker, Ann. Bot. (König & Sims) 1: 224. 1804; Baker, Handb. Irid. 157. 1892, Fl. Cap. 6: 73. 1896, non sensu Baker (intended for *G. imbricata* sensu lato); Goldblatt & Barnard, J. S. African Bot. 36: 296–298. 1970. *Ixia inflexa* de la Roche. Descr. Pl. Aliq. Nov. 15. 1766. *Hesperantha inflexa* (de la Roche) Foster, Contr. Gray Herb. 135: 77. 1941, excl. basion. [name misapplied to *Hesperantha vaginata* (Sweet) Goldbl.]. TYPE: South Africa. Cape: Cape Peninsula, *Barker 3869* [neotype, BOL, designated by Goldblatt & Barnard (1970); isoneotype, NBG]. FIGURE 81.

Ixia hirta Thunb., Diss. de *Ixia* no. 6. 1783, hom. illeg. superfl. pro *I. inflexa* de la Roche. *Geissorhiza hirta* (Thunb.) Ker, Ann. Bot. (König & Sims) 1: 224. 1804; Baker, Handb. Irid. 155. 1892, Fl. Cap. 6: 71. 1896, nom. illeg. basion. illeg. superfl.

Ixia erosa Salisb., Prod. 36. 1796. *Geissorhiza erosa* (Salisb.) Foster, Contr. Gray Herb. 135: 52. 1941. TYPE: South Africa. Origin unknown: cultivated in England [location of type unknown, possible isotype at G (Herb. DC)].

Ixia ciliaris Salisb. ex Ker, Bot. Mag. 18: sub. tab. 672. 1803, nom. nud. in syn. [*Ixia ciliaris* and therefore *G. ciliaris* are apparently based on a specimen collected by *Auge s.n.* (BM), annotated "*Ixia ciliaris* Salisb. Prod." (probably in Salisbury's hand). It is the large, red- or purple-flowered form of *G. inflexa.*]

Geissorhiza (as *Gissorhiza*) *ciliaris* Salisb., Trans. Hort. Soc. London 1: 321. 1812, nom. nud. (apparently intended as a combination in *Geissorhiza* of "*Ixia ciliaris* Salisb., Prod. 36. 1796," a name never published—possibly Salisbury changed the epithet in print: *Ixia erosa* Salisb., which is conspecific, appears on the page cited in his Prodromus).

Geissorhiza ciliaris (Ker) Jackson, Index Kew. 1: 1006. 1895, nom. nud. basion. inval.

Geissorhiza rosea Ecklon, Topogr. Verz. Pflanzensamml. Ecklon 20. 1827. TYPE: South Africa. Cape: near Tulbagh, cultivated in Cape Town, *Ecklon s.n.* [lectotype, S, designated by Nordenstam (1970)].

Geissorhiza candida Ecklon, Topogr. Verz. Pflanzensamml. Ecklon 21. 1827. TYPE: South Africa. Cape: Hottentots Holland, *Zeyher s.n.* (lectotype, S).

Geissorhiza quinquangularis Ecklon ex Klatt, Linnaea

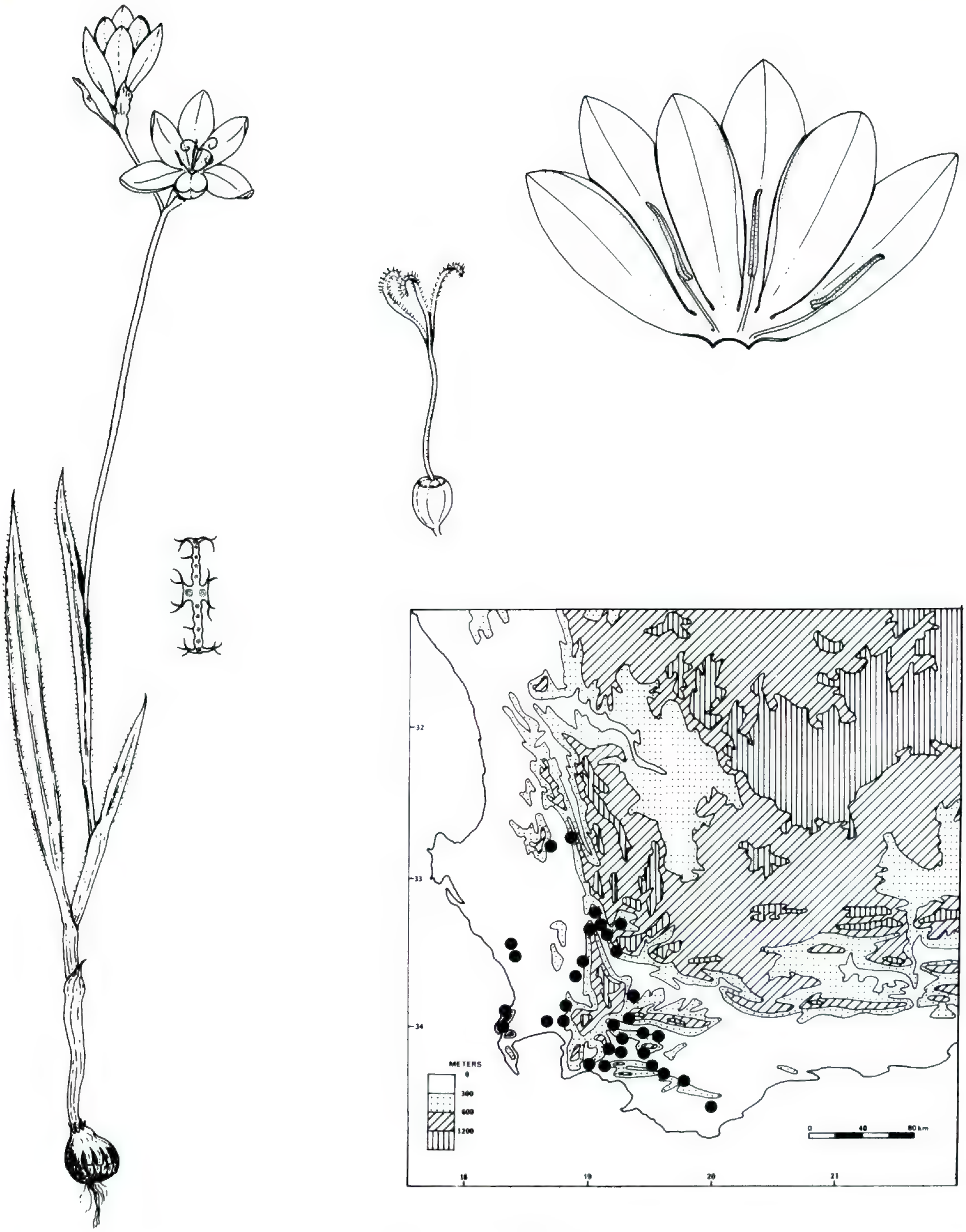


FIGURE 81. Morphology and distribution of *Geissorhiza inflexa*. Habit life size; opened flower and gynoecium ×2; leaf section much enlarged (*Goldblatt 5643*, N of Bot River).

34: 654. 1865; Foster, Contr. Gray Herb. 135: 53–54. 1941, nom. superfl. pro *G. rosea* Ecklon if this species is accepted as validly described, as here. [Specimens cited in the description are: *Ecklon & Zeyher Irid. 214* (Caledon Zwarteberg), the sheet designated by Foster (1941: 54) as the lectotype; *Ecklon & Zeyher Irid. 215*; *Ecklon & Zeyher Irid. 296*; and *Lalande s.n.*]

Hesperantha kermesina Klatt, Abh. Naturf. Ges. Halle 15: 395 (Erg. 61). 1882. *Geissorhiza erosa* var.

kermesina (Klatt) Foster, Contr. Gray Herb. 135: 53. 1941. TYPE: South Africa. Cape: between Paarl and Pont, *Drège 8480* [lectotype, B, effectively designated by Foster (1941: 53); isolectotypes, B, BM, G, K, L, MO, S].

Hesperantha quinquangularis Ecklon, Topogr. Verz. Pflanzensamml. Ecklon 23. 1827, nom. nud.

Geissorhiza graminifolia Baker, Handb. Irid. 155. 1892, Fl. Cap. 6: 70. 1896. TYPE: South Africa. Cape: near Swellendam, *Drège 3496* (lectotype, K, here designated; isolectotypes, B, E, G, L, MO, P); near George, *Burchell 6088* (syntype, K = *G. heterostyla*).

Geissorhiza graminifolia var. *bicolor* Baker, Handb. Irid. 155. 1892, Fl. Cap. 6: 70. 1896. TYPE: South Africa. Cape: Hout Bay, *MacOwan in Herb. Norm. Austr. Afr. 261* (lectotype, K, here designated; isolectotypes, B, BOL, G, SAM; syntypes, see Flora Cap. 6: 70. 1896).

Geissorhiza quinquangularis var. *atrofaux* Foster, Contr. Gray Herb. 135: 55. 1941. TYPE: South Africa. Cape: Piketberg, *Schlechter 5210* (holotype, B; isotypes, B, BM, G, K, SAM, W, Z).

Geissorhiza pilosa Pappe ms. [Cape Flats, *Pappe s.n.* (SAM)].

Plants (5–)12–30(–40) cm high. *Corm* symmetric, 7–12 mm diam., tunics blackish, imbricate, the outer layers notched regularly below into segments. *Cataphyll* membranous, dark above. *Leaves* 3, usually half to two-thirds as long as the stem, sometimes exceeding the spike linear-ensiform, (1.5–)3–4(–10) mm wide, the margins extended outward at right angles to the blade, the midrib also raised and winged, the edges of the margins and midrib and sometimes other larger veins ciliate-pubescent, the lower two leaves basal, the uppermost basal or more often cauline, sheathing for most of its length, the sheath ribbed and ciliate-pubescent, slightly inflated. *Stem* erect, smooth, sheathed below by the uppermost leaf, rarely branched. *Spike* (1–)2–6-flowered, flexed at the base; *bracts* membranous, dry, reddish brown, occasionally greenish below, 7–15(–22) mm long, the inner somewhat smaller than the outer. *Flowers* stellate, either purple, pink, red, or white, cream or pale yellow and then usually red-flushed on the reverse of the outer tepals and occasionally dark in the center; *perianth tube* short 1–2.5 mm long; *tepals* (8–)10–18(–24) mm long, obovate, 8–10 mm at widest. *Filaments* 4–7 mm long, equal; *anthers* (2.5–)3–6(–8) mm long. *Ovary* 2–3 mm long, *style* dividing near the apex of the anthers, branches ca. 4–5 mm long, recurved above. *Capsule* globose to oblong, 3–6 mm long. *Chromosome number*, $2n = 26$ (*Goldblatt 2497, 6173*), $2n = 26 + 1B$ (*Goldblatt 5228*).

Flowering time. August to September

Distribution. Southwestern Cape, from Bredasdorp and Swellendam in the east to the Cape Peninsula and north to Piketberg, extending inland in the Tulbagh and Worcester valleys. Figure 81.

Geissorhiza inflexa was described in 1766 by Daniel de la Roche in an important publication, actually his doctoral dissertation, in which 20 species of Cape Iridaceae were described. Placed in the genus *Ixia*, it was misinterpreted by Baker (1892, 1896) who cited specimens of *G. imbricata* under this name and by Foster (1948) who confused it with the large yellow-flowered *Hesperantha vaginata* from the Calvinia district in the northern Cape. Authentic material at the Leiden Herbarium (Goldblatt & Barnard, 1970) makes it quite clear that *I. inflexa* is a species of *Geissorhiza*, as realized by Ker in 1804. It is conspecific with what was long known as *G. quinquangularis*, or *G. graminifolia*. A neotype, *Barker 3869* from the Cape Peninsula, a good match for the material at Leiden, was designated by Goldblatt and Barnard.

The species is common in the southwestern Cape on clay and shale slopes and sometimes is found on very stony ground. It extends from Bredasdorp and Swellendam in the east to the Cape Peninsula and Mamre and northward to the Piketberg district with inland extensions into the Tulbagh and Worcester valleys. It belongs to section *Ciliata* of subgenus *Geissorhiza*, the species of which have leaves with a raised margin which extends at right angles to the blade and itself has ciliate edges. The midrib is also slightly raised and winged with ciliate edges. Occasionally one or more secondary pairs of veins may also be ciliate. Of the group, *G. inflexa* seems one of the more specialized, having few flowered spikes and only occasionally branched stems. It always has three leaves and lacks the stem bract found in some of the other species of the group. The flowers are moderate to large in size, and range in color from cream to pale yellow with pink or red on the reverse of the outer tepals to shades of pink, red, or purple. *Geissorhiza heterostyla*, a southern Cape species that extends north into the western Karoo is closely allied, but can readily be distinguished by its one filament much shorter than the others, a more branched inflorescence, and conspicuous dry stem bracts below the spike.

There is a tendency for reduction in flower size

and narrowing of the leaves in populations of *Geissorhiza inflexa* towards the east of its range, south and east of Caledon. At Bredasdorp specimens seem very different from the robust plants that occur at Tulbagh, and it is easy to see why earlier authors should have recognized these as separate species. However, the narrowest leaved form which is found at Bredasdorp, with leaves 1–2 mm wide and flowers with tepals ca. 9 mm long (*Wasserfall 376, Barker 2527, 2475, Compton 9094*) is connected through a series of intermediates to the type specimens of *G. quinquangularis* (leaves 3 mm wide, tepals 15 mm long) and *G. inflexa* (leaves 4–6 mm wide, tepals to 12 mm long). The latter specimen in turn matches, except in flower color, several collections from Stellenbosch, Mamre, and Tulbagh, with purple or red flowers [e.g., *Leighton 1338, Zeyher s.n.* (SAM 20861), *Mathews 10, Grant 2459* (leaves 5–8 mm wide, tepals to 14 mm long)] which are clearly conspecific with such strikingly robust specimens as *Lewis 5335, 5740, MacOwan s.n.* (Herb. Norm. Austr. Afr. 590) (leaves 5–10 mm wide, tepals 18–20 mm long).

Traditionally the red, pink, or purple and robust form of *Geissorhiza inflexa* has been regarded as a species distinct from plants with white to cream flowers marked red on the reverse of the outer tepals. Baker (1892, 1896) recognized pink- to purple-flowered plants as *G. hirta* (an illegitimate name) and the paler flowered and often slender plants as *G. graminifolia*. The latter is actually based on two collections, one, *Burchell 6088*, is *G. heterostyla* and the other, a Drège collection, here designated the lectotype, matches several other specimens of *G. inflexa* cited in "Flora Capensis." The Drège collection corresponds closely to the type material of *G. quinquangularis* Ecklon ex Klatt, a much earlier name, and the one used by Foster in his monograph for this form. Foster used the name *G. erosa* for the robust, and red- to purple-flowered plants as he realized *G. hirta* was superfluous and illegitimate.

The recognition of the two forms as separate species seems unjustified, as it is based largely on color differences. Specimens with cream flowers from the Cape Peninsula, and north of Cape Town, as well as the type collection of *G. quinquangularis* match some of the less robust, red-flowered specimens of *G. erosa-hirta* in every respect except flower color, and separation of species on color differences alone is unacceptable, and especially since cream-flowered specimens occur occasionally in populations of the red-flowered form from Tulbagh (*Lewis 5738, Garside 1541*). These two forms are consequently united here in one species, the earliest name for which is *G. inflexa*. There is obviously intense selection for red flower color in the Tulbagh valley, and several species of *Iridaceae*, elsewhere white- or blue-flowered, have flowers in red to purple colors here (e.g., *Sparaxis grandiflora, Babiana villosa*, and *Galaxia versicolor*).

Similar selection for a cream (to pale yellow) flower with a dark center and throat is evident along the coastal belt north of Cape Town especially in the Piketberg-Porterville area and populations of *Geissorhiza inflexa* here also have pale flowers with a dark center. This form was recognized by Foster (1941) as *G. inflexa* var. *atrofaux*. It seems to me no more than a minor color variant, and not worth taxonomic recognition. Loubser has recorded probable hybridization between this form of *G. inflexa* and *G. tulbaghensis* where they occur together on a farm northwest of Porterville, also in association with *G. secunda*. *Loubser 2188* and *2104* have large flowers with a red throat, a character of *G. tulbaghensis*, while *Loubser 2102* has self-colored flowers.

Specimens examined. SOUTH AFRICA. CAPE: 3218 (Clanwilliam) Piketberg Mt. (DC), *Schlechter 5210* (B, BM, G, K, SAM, W, Z); Nurust farm 8 mi. NW of Porterville (DD), *Loubser 2102* (BOL), *2188* (NBG).

3318 (Cape Town) Contreberg slopes (AD), *Pillans 6945* (BOL); Mamre hills, *Barker 1813* (NBG); Groenekloof, *Zeyher s.n.* (SAM 20861), *MacOwan in Herb. Norm. Austr. Afr. 590* (B, BOL, G, GH, K, SAM); near Cape Town (CD), *H. Bolus 4805* (BOL, K); Signal Hill, *Barker 405* (NBG), *Wolley Dod 521* (BM, BOL, K); Signal Hill, above Tamboers Kloof, *Michell s.n.* (NBG), *Salter 7629* (CT, SAM); Lions Head, *Ecklon 312* (B, E, K, M, MO, S, Z); Lions Rump, *Thode 8457* (STE); Table Mt., *MacOwan s.n.* (S); Wellington (DB), *Grant 2376* (BOL, M, MO); near Wellington, *Dümmer 2840* (E); Stellenbosch (DD), *Ecklon & Zeyher Irid. 215* (87) (FI, G, MO); near Stellenbosch, *Lightfoot s.n.* (BOL 3194); between Paarl and Pont, *Drège 8480* (B, BM, G, K, L, MO, S); Onderpapagaisberg, lower slopes, *Taylor 6882* (STE); Jonkershoek, *Garside 1531* (K); Jonkershoek valley, *Lewis 1995* (SAM); Stellenbosch, *Duthie 585* (BOL), *Worsdell s.n.* (K); Paarl, *Loubser 467* (NBG).

3319 (Worcester) Tulbagh (AC), *Hall 1426* (NBG), *Grant 2459* (MO), *Marloth 7801* (PRE), *8909* (PRE), *Garside 1541* (K), *Rogers 11097* (Z), *MacOwan 2678* (E, K); 2 mi. S of Tulbagh, stony clay flats, *Lewis 5740* (NBG); S-facing hill slopes on clay at Tulbagh, *Lewis 5738* (NBG, STE); lower slopes of the Witsenberg, *Leighton 1338* (BOL, NBG); foot of the Witsenberg near Michells Pass, *Goldblatt 4077* (MO); Tulbagh cemetery, *Goldblatt 5228* (MO); 1 mi. S of Tulbagh

Road Station, *Goldblatt 304* (MO); near Artois, *H. Bolus s.n.* (BOL); Ceres, *Reyneke 12* (BOL); Ceres Road (Wolseley), *Schlechter 8975* (B); 3 mi. from Hermon on Tulbagh road, *Marsh 738* (PRE, STE); Slanghoek valley (CA), *Barker 9470* (NBG); shale hills between Villiersdorp and Brandvlei (CD), *Goldblatt 6203* (MO).

3418 (Simonstown) near Hout Bay neck (AB), *MacOwan in Herb. Norm. Aust. Afr. 261* (B, BM, BOL, G, K, SAM, W) = *MacOwan 2632* (SAM); Cape Flats (BA), *Pappe s.n.* (K, SAM); Hottentots Holland (BB), *Ecklon & Zeyher Irid. 214* (91.8) (K, SAM); wet flats at Gordons Bay, *H. Bolus 9939* (BOL, K, PRE, Z); near Faure at Macassar Beach turnoff, *Jackson s.n.* (NBG 88444); near Oudebos farm, Palmiet River Valley, shale band (BD), *Boucher 1894* (PRE, STE).

3419 (Caledon) N of Bot River (AA), *Goldblatt 5643* (BR, MO, US, WAG), *Goldblatt 4982A* (MO); Bot River-Caledon road via Goedvertrou, *Goldblatt 3996* (MO); clay slope W of Eseljag Pass on road to Queen Anne, *Goldblatt 2497* (K, MO, PRE, S, US, WAG); stony clay flats S of Villiersdorp at Theewater farms turnoff (AB), *Goldblatt 4015* (MO, NBG); between Caledon and Villiersdorp, at Riviersonderend bridge, *Salter 4793* (BM, BOL, K); Caledon (AB), *Barker 2495* (NBG); commonage below Zwartberg, Caledon, *Guthrie s.n.* (BOL); lower S slopes of Swartberg, Caledon, *Esterhuysen 32670* (BOL, MO), *Ecklon & Zeyher Irid. 214* (51.8) (B, BR, E, FI, G, LD, W, Z), *Schlechter 5561* (B, PRE, Z); Caledon Zwartberg, slopes above Gardens, *Goldblatt 5896* (MO, WAG); clay slope on W outskirts of Caledon, *Goldblatt 6173* (MO); 18.4 km SW of Greyton, *Acocks 24340* (K, MO, PRE); Albertyn-Caledon road near Leeurivier (AC), *Goldblatt 4837* (MO, US); Fernkloof, Hermanus (AD), *Goldblatt 5176* (MO, PRE); Fairfield (BD), *Lewis 5286* (NBG); NE of Sandys Glen, near Fairfield, *Goldblatt 4848* (MO); The Poort, SW of Bredasdorp (DB), *Wasserfall 378* (NBG), *Goldblatt 4862A* (MO), *Barker 2475* (NBG), *2527* (NBG), *Acocks 24238* (EA, STE); Poort hills, Bredasdorp, *Compton 9094* (NBG).

WITHOUT PRECISE LOCALITY: Breede River, near Swellendam, *Drège 3496* (B, BM, E, G, K, L, MO); Cape of Good Hope (C.B.S.), Herb. Burman *s.n.* (G), *Thunberg s.n.* (*Ixia hirta*) (S "Herb. Montin," UPS), *Roxburgh s.n.* (BM), *Pappe s.n.* (BM), *Prior s.n.* (K).

FIGURE 82. Morphology and distribution of *Geissorhiza erubescens*. Habit ×0.5; flower life size; leaf section much enlarged (*Goldblatt 6396*, Pakhuis Pass).

80. Geissorhiza erubescens Goldbl., sp. nov. TYPE: South Africa. Cape: Pakhuis Pass, on shale slopes near top of pass, *Goldblatt 6396* (holotype, MO; isotypes, K, NBG, PRE, S, WAG). FIGURE 82.

Planta (5–)8–15 cm alta, foliis 3, duobus inferioribus basalibus erectis linearibus, floribus (1–)3–7, albis, rubris in reverso tepalorum exteriorum, tubo 1.5–2 mm longo, tepalis 8–12 mm longis, filamentis aequalibus, antheris 2.5–3 mm longis, stylo diviso prope apicem antherarum, ramis recurvatis.

Plants (5–)8–15 cm high. *Corm* more or less globose, obliquely flattened below, 5–12 mm diam., tunics blackish, imbricate, notched regularly below into segments. *Cataphyll* firm, brownish, persistent, and accumulating with leaf bases in a fibrous neck around the stem base in older individuals. *Leaves* 3, linear and erect, 2–3 mm wide, half to two-thirds as long as the stem, the margins raised with wings extending at right angles to the blade, the midrib also raised and winged, minutely ciliate to visibly pubescent on the edges of the margins, midrib, and sometimes other veins, the lower two leaves basal, the uppermost leaf largest and inserted in the middle part of the stem, sheathing below. *Stem* erect, ciliate to pubescent below the third leaf, ciliate or smooth above, simple or 1-branched. *Spike* flexed at the base, (1–)3–7-flowered, flexuose; *bracts* membranous and greenish to transparent below, rust brown above, 6–8 mm long, flexed outward in the midline, the inner shorter than the outer. *Flowers* stellate, creamy white, bright red on the reverse of the outer tepals; *perianth*

tube 1.5–2 mm long, much shorter than the bracts; *tepals* 8–12 mm long, ovate-elliptic, 3–4 mm wide. *Filaments* equal, ca. 3 mm long; *anthers* 2.5–3 mm long, cream. *Ovary* 1–2 mm long, *style* dividing at the apex of the anthers, branches recurved. *Capsule* unknown. *Chromosome number*, $2n = 26$ (*Goldblatt 6396*).

Flowering time. September.

Distribution. Known only from Pakhuis Pass, common on the shale band, especially after fires. Figure 82.

Geissorhiza erubescens is a distinctive small-flowered species of section *Ciliata*, probably most closely allied to the southwestern Cape *G. inflexa* and to *G. leipoldtii* which occurs in the same general area as *G. erubescens*. It can be distinguished by the unusual sheath of fibers around the stem base, at least in older individuals; relatively small flowers with tepals 8–12 mm long; strongly winged leaf margins; and its lightly ciliate-pubescent stem, at least below the uppermost leaf. It is perhaps closest to *G. leipoldtii* which sometimes has unequal stamens and typically larger flowers, the tepals (13–)18–28 mm long, without the deep red markings on the reverse of the outer tepals characteristic of *G. erubescens*. It also bears some resemblance to the Nieuwoudtville and Gifberg species, *G. divaricata*, but this typically has distinctive, dry stem bracts and always has a smooth stem.

Geissorhiza erubescens has been collected only in the upper part of Pakhuis Pass in the shale band, growing in a light sandy clay gravel. When I found it in 1981 it was flowering in profusion in the season following a veld fire. It seems likely that it flowers only in the spring after a burn.

Specimens examined. SOUTH AFRICA. CAPE: 3219 (Wuppertal) E slopes of Pakhuis Pass (AA), *Compton 19964* (NBG); Pakhuis Pass, near top of pass on shale slopes, *Goldblatt 6396* (K, MO, NBG, PRE, S, US, WAG), *Goldblatt 6397* (MO).

FIGURE 83. Morphology and distribution of *Geissorhiza leipoldtii*. Habit ×0.5; flower life size; leaf section much enlarged (*Goldblatt 6165*, S of Clanwilliam).

81. Geissorhiza leipoldtii Foster, Contr. Gray Herb. 135: 47. 1941. TYPE: South Africa. Cape: Pakhuis-Wuppertal road, *Leipoldt s.n.* (holotype, BOL 20778 in K; isotype, BOL). FIGURE 83.

Geissorhiza ixioides Schltr. ex Foster, Contr. Gray Herb. 135: 43–44. 1941. TYPE: South Africa. Cape: "Agtertuin, in collibus," *Schlechter 10866* (holotype, B; isotypes, BM, BOL, BR, E, G, K, L, LD, MO, P, PH, PRE, S, Z).

Plants (12–)16–30 cm high. *Corm* symmetric, globose, 5–8 mm diam., tunics dark brown to blackish, imbricate, the outer layers regularly notched below into segments. *Cataphyll* solitary, membranous, brownish above. *Leaves* 3, linear to ensiform, 3–5 mm wide, usually shorter than the stem, apparently plane but the margins raised at right angles to the blade and winged, ciliate along the edges, the midrib also slightly raised and winged, sparsely ciliate along the edges, the lower two leaves basal, the uppermost inserted above the ground and sheathing for at least half its length. *Stem* erect, sparsely puberulent to ciliate, simple or 1-branched. *Spike* flexed at the base of the spike, 2–6-flowered, flexuose; *bracts* membranous, dry and pale brown above, greenish below, 10–16(–22) mm long, the inner smaller than the outer. *Flowers* somewhat cupped,

white or pale pink to purple (often becoming pink with age), apparently dark in the throat in the type population of *G. ixioides*; *perianth tube* 1.5–2 mm long; *tepals* narrowly obovate, (13–)18–28 mm long, 7–10 mm wide. *Filaments* either equal and 5–6 mm long or unequal with one shorter and 2.5 mm long; *anthers* 6–8 mm long, yellow. *Ovary* ca. 2 mm long, *style* dividing towards the apex of the anthers, branches 3–6 mm, recurved. *Capsules* unknown. *Chromosome number*, unknown.

Flowering time. August to September.

Distribution. Shale soils especially on south-facing slopes in the Olifants River Valley and the mountains east of Pakhuis Pass. Figure 83.

Geissorhiza leipoldtii is native to the arid hills of the Olifants River and northern Cedarberg Mountains and its foothills east of Pakhuis Pass. It is evidently allied to the southwestern Cape species *G. inflexa* and it resembles especially the larger flowered forms of this species. It can, however, readily be recognized by its puberulous or ciliate stems, only sparsely ciliate leaves and often unequal stamens. *Geissorhiza erubescens* is undoubtedly closely allied to *G. leipoldtii*. This endemic of the Pakhuis Mountains has small, white to cream flowers with deep red markings on the reverse of the outer tepals, a distinctive fibrous sheath around the stem base and consistently equal filaments. *Geissorhiza leipoldtii* is poorly collected, probably because plants bloom well only in the years when more favorable rains have fallen. Included in the species are two collections made in the wet spring of 1974 on the upper slopes of Biedouw Pass (*Mauve & Oliver 82, Goldblatt 2540*) which are unusually robust and have very large flowers, perhaps owing to particularly good rainfall that year.

Geissorhiza ixioides Foster is here reduced to synonymy. This species was recognized on the basis of its smaller flowers (tepals ca. 13 mm long) with a dark center (possibly an artifact of drying), supposed short style and equal stamens, in contrast to the supposed unequal stamens of *G. leipoldtii*. A tendency can be detected in some recent collections of *G. leipoldtii* to develop a dark color in the center of the flower but this character has no taxonomic significance. Foster described the filaments of *G. leipoldtii* as unequal, one being shorter but examination of the type collection at my disposal including the ample material at BOL, not seen by Foster, has shown the filaments of the type of *G. leipoldtii* to be essentially equal, while type material of *G. ixioides* has a style of normal length.

A collection from the Olifants River Valley near Clanwilliam, *Goldblatt 6165*, is unusual in having distinctly unequal filaments, one being about half the length of the other two. In the absence of any other differences, this form is included in *Geissorhiza leipoldtii*.

Specimens examined. SOUTH AFRICA. CAPE: 3218 (Clanwilliam) 10 km S of Clanwilliam, clay bank (BB), *Goldblatt 6165*.

3219 (Wuppertal) Pakhuis-Wuppertal road (AA), *Leipoldt s.n.* (BOL 20778, K, SAM); slopes above Welbedacht, *Lewis 5222* (NBG, STE); road to Wuppertal, near Lubbe's farm, *Martin 808* (NBG); Pakhuisberg, *Schlechter 8621* (B, BM, BOL, BR, E, G, H, K, L, LD, MO, P, PH, PRE, S, Z), *313a* (PRE); Agtertuin, *Schlechter 10866* (B, BM, BOL, BR, G, K, L, MO, P, PH, PRE, S, Z); top of Biedouw Pass, SE slopes, *Mauve & Oliver 82* (K, MO, PRE, S); *Goldblatt 2540* (K, MO, NBG, S, US, WAG); Cedarberg Forest Reserve, Langrug, 1,000 ft. (AC), *Viviers 584* (MO); Matjesrivier, Cedarberg (AD), *Wagener 214* (NBG).

SPECIES INCOMPLETELY UNDERSTOOD

The following represent apparently undescribed species, but the material available is too fragmentary and incompletely known to form the basis for the description of a new species.

1. *Geissorhiza* sp. 1 (*Rogers 28746*, Z).

A collection of only two plants made by F. A. Rogers at Ceres clearly represents a species not included in this revision. The corm appears to have imbricate tunics which places the species in subgenus *Geissorhiza*. Other significant characteristics include two basal, and a third cauline and partly sheathing, narrow and linear, foliage leaves that have thickened margins and midrib and thus are narrowly 2-grooved on each surface; a puberulent, unbranched stem; an apparently membranous bract in the upper part of the stem; and spikes of 2 long-tubed flowers. The plants are 15–20 mm high and very slender, the leaves about 1 mm wide and half as long as the stem. The flowers appear to be salver shaped, with a tube 9–12 mm long and horizontally extended tepals ca. 16 mm long. The stamens are unequal, the two longer with filaments 5 mm long and a shorter one with a filament 2.5 mm long. The style is of the *Geissorhiza* type and reaches to about the apex of the anthers and has 3 spreading branches.

The morphology of the leaves and stem, as well as the flower with unequal stamens all sug-

gest that this species is correctly assigned to subgenus *Geissorhiza,* in which unequal stamens are common and pubescent stems not unusual. The affinities of the species are most likely with section *Monticola,* most species of which have unequal stamens, but usually branched stems. However, stem pubescence is unknown in the section. Further material is needed before the species can be described and its relationships more adequately assessed. Locality information is unfortunately limited to Ceres and the altitude 1,400 ft. Ceres may represent the town itself, the immediate surroundings or the district that extends well to the north. The altitude suggests that the species grows on lower to middle mountain slopes.

2. *Geissorhiza* sp. 2 (*Stokoe s.n.,* SAM 65812).

A collection of a small species, made in December 1952 by T. P. Stokoe at Oudebosch in the Palmiet River Mountains, appears to represent either an undescribed species or a very aberrant form of a known one. The plants are 10–15 cm high, have linear, plane leaves and smooth, simple or 1-branched stems with solitary flowered spikes. The corms are small and apparently have soft-textured tunics that do not accumulate to any degree, and it is not possible to determine whether the tunics are concentric or imbricate. Accordingly, the species cannot be assigned to subgenus with certainty. The overall appearance of the plants and the soft plane leaves, however, suggests that the species belongs in section and subgenus *Weihea.* The branching pattern is unusual. The branches are almost equal in length and so appear dichotomous. This type of branching is known in *Geissorhiza* only in *G. geminata,* also section *Weihea* and it is to this species that *G.* sp. 2 is assumed to be allied if not simply a depauperate form of *G. geminata.* More material of the species is needed before a final decision can be taken on the status of this collection.

EXCLUDED SPECIES

Geissorhiza abyssinica R. Br. ex A. Richard, Tent. Fl. Abyss. 308. 1850.
= *Lapeirousia abyssinica* (R. Br. ex A. Richard) Baker (Baker, 1898; Cufodontis, 1972).

Geissorhiza albens E. Mey. in Drège, Zwei Pflanzengeogr. Dokum. 187. 1843, nom. nud.
= *Gladiolus debilis* Ker (Lewis et al., 1972).

Geissorhiza alpina Hook. f., J. Linn. Soc., Bot. 7: 233. 1864.
= *Hesperantha petitiana* (A. Richard) Baker.

Geissorhiza ambongensis H. Perrier, Notul. Syst. (Paris) 8: 130. 1939.
= ? *Tritonia* sp. (Goldblatt, 1982b).

Geissorhiza anemonaeflora (Jacq.) Klatt, Linnaea 34: 657. 1866. *Ixia anemonaeflora* Jacq. Icon. Pl. Rar. 2: tab. 273. 1793.
= *Ixia campanulata* Houtt. fide Lewis (1962).

Geissorhiza bojeri Baker, J. Bot. 14: 239. 1876.
= *Gladiolus bojeri* (Baker) Goldbl. (Goldblatt, 1982b).

Geissorhiza briartii Wildem. & Durand, Bull. Soc. Roy. Bot. Belgique 39: 105. 1900.
= *Lapeirousia erythrantha* (Klotzsch ex Klatt) Baker var. *briartii* (Wildem. & Durand) Geerinck, Lisowski, Malaisse & Symoens (Geerinck et al., 1972).

Geissorhiza erecta Baker, J. Bot. n.s. 5: 238. 1876.
= *Hesperantha erecta* (Baker) Benth. ex Baker (Goldblatt, 1984).

Geissorhiza gracilis Baker, Handb. Irid. 155. 1892.
= *Gladiolus parvulus* Schltr. (Lewis et al., 1972).

Geissorhiza grandis Hook. f., Bot. Mag. 96: tab. 5877. 1870.
= *Gladiolus floribundus* Jacq. subsp. *milleri* (Ker) Oberm. (Lewis et al., 1972).

Geissorhiza latifolia (de la Roche) Baker, J. Linn. Soc., Bot. 16: 94. 1878.
= *Ixia latifolia* de la Roche (Lewis, 1962; Goldblatt & Barnard, 1970).

Geissorhiza longituba Klatt, Linnaea 35: 383. 1867–1868.
= *Hesperantha longituba* (Klatt) Baker (Goldblatt, 1984).

Geissorhiza lutea Ecklon, Topogr. Verz. Pflanzensamml. Ecklon 21. 1827, nom. nud.
= *Hesperantha falcata* (L. f.) Ker (Goldblatt, 1984) (syn. *Hesperantha lutea* Ecklon ex Baker).

Geissorhiza macra Baker, Bull. Herb. Boissier, Ser. 2, 4: 1004. 1904. TYPE: South Africa. Transvaal: Mt. Malchachi, *Jacottet s.n.* (G, not seen; GH, photo).
= *Hesperantha* sp., the fairly large flowers are borne singly on the stems.

Geissorhiza minima Baker, J. Bot. n.s. 5: 239. 1876.
= *Hesperantha minima* (Baker) Foster (Foster, 1948; Goldblatt, 1984).

Geissorhiza patersoniae L. Bolus, Ann. Bolus Herb. 1: 132. 1915.

= *Gladiolus stellatus* Lewis (Lewis, 1966; Lewis et al., 1972).

Geissorhiza pauciflora Baker, Bull. Herb. Boissier, Ser. 2, 10: 1004. 1904.
= *Hesperantha falcata* (L. f.) Ker (Goldblatt, 1984).

Geissorhiza quadrangula (de la Roche) Ker, Irid. Gen. 88. 1827. *Ixia quadrangula* de la Roche, Descr. Pl. Aliq. Nov. 16. 1766.
= *Gladiolus quadrangulus* (de la Roche) Barnard (Goldblatt & Barnard, 1970).

Geissorhiza recurvifolia (Poiret) Klatt sensu Klatt, Linnaea 34: 655. 1866. *Ixia recurvifolia* [sic] Poiret in Lam., Encycl. Suppl 3(1): 201. 1813, nom. var. vel. nom. superfl. pro *Ixia recurva* Red., Liliac. 5(42): tab. 251, f. 2. 1809.
= *Romulea* cf. *flava* (Lam.) De Vos (De Vos, 1972).

Geissorhiza schlechteri Baker, Bull. Herb. Boissier, Ser. 2, 9: 43. 1901.
= *Hesperantha schlechteri* (Baker) Foster (Foster, 1936).

Geissorhiza sublutea (Lam.) Ker, Ann. Bot. (König & Sims) 1: 224. 1804. *Ixia sublutea* Lam., Encycl. 3: 335. 1789.
= *Romulea triflora* (Burm. f.) N. E. Brown (De Vos, 1972).

Geissorhiza vaginata Sweet, Brit. Flow. Gard., Ser. 1, tab. 138. 1826.
= *Hesperantha vaginata* (Sweet) Goldbl. (Goldblatt & Barnard, 1970; Goldblatt, 1984).

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NOTES

A NEW *SYNGONANTHUS* (ERIOCAULACEAE) FROM SOUTHERN MEXICO

While preparing a treatment of the Eriocaulaceae for "Flora Mesoamericana," I discovered two recent collections of a distinctive species of *Syngonanthus* from the State of Chiapas in southern Mexico here described as *S. davidsei* Huft. This is only the second species of the genus to be found in Mexico. *Syngonanthus caulescens* has been collected in bogs near Minatitlán, Veracruz (2 Feb. 1892, *Smith 354,* MO), and is also known from Costa Rica and northern South America. The only other species of this largely South American genus that are known from continental North America are *S. flavidulus* (Michx.) Ruhl. of the southeastern United States, *S. pittieri* from Panama, and four poorly-known species endemic to Belize.

Syngonanthus davidsei Huft, sp. nov. TYPE: Mexico. Chiapas: Municipio of Ixtapa, grassy flats with *Quercus, Acacia,* and *Byrsonima* near Ixtapa, 915 m, 1 Nov. 1981, *Breedlove & Davidse 54339* (holotype, CAS!; F neg. no. 59185; isotypes, to be distributed to ENCB, MEXU, MO, not seen).

Herbae parvae perennes, acaulescentes. Folia lineari-lanceolata, modice strigosa, apice acuminata. Pedunculi aliquot, terminales, glanduloso-pilosi. Capitula solitaria, aureo-brunnea; bracteae involucrales late ovatae, naviculares, aureo-brunneae, glabrae, apice obtusae vel parum acutae; bracteolae receptaculares nullae. Flores stipitati, stipitibus basi longiciliatis, ceterum glabri; sepala ♂ late obovato-falcata, aureo-brunnea; sepala ♀ elliptico-oblonga, basi alba, apice aureo-brunnea; petala ♀ anguste oblonga, sepalis parum breviora, alba, basi libera, versus apicem conniventia vel leviter connata.

Small perennial *herb,* monoecious, acaulescent. *Leaves* tufted, spreading or recurved, often flat on the ground, linear-lanceolate, 1–1.5 cm long, 0.8–1.2 mm wide, moderately strigose, the apex acuminate. *Peduncles* several, terminal, 6–17 cm long, slender, glandular-pilose, the hairs spreading; sheath 12–20 mm long, appressed, densely glandular-pilose, the apex long-acuminate. *Heads* solitary, hemispherical, golden brown, glabrous, 2.5–5 mm diam.; involucral bracts broadly ovate, navicular, 1.8–2 mm long, 0.8–1 mm wide, golden brown, glabrous, the apex obtuse to acute: receptacle flat, glabrous; receptacular bracts lacking. *Staminate florets* stipitate, the stipe 0.3–0.5 mm long, long-ciliate at base; sepals 3, free, broadly obovate-falcate, navicular, ca. 1 mm long, ca. 0.5 mm wide, glabrous, golden brown, the apex obtuse to acute; petals connate into a narrow, glabrous, stramineous tube, the apex with 3 short lobes; stamens 3, the anthers white. *Pistillate florets* stipitate, the stipe ca. 0.5 mm long, long-ciliate at base; sepals 3, free, elliptic-oblong, 1.3–1.5 mm long, ca. 0.4 mm wide, glabrous, white toward base, golden brown toward apex, the apex acute; petals 3, narrowly oblong, slightly shorter than the sepals, glabrous, white, connivent or loosely connate near the apex; ovary 3-locular, glabrous; styles 3, 0.8–1 mm long, united ca. two-thirds their length; seeds not seen.

Additional specimen examined. MEXICO. CHIAPAS: Municipio of La Trinitaria, 10 km E of La Trinitaria on road to Lagos de Montebello National Park, sandy flats with *Pinus* and *Quercus,* 1,555 m, 7 Nov. 1981, *Breedlove & Davidse 54973* (CAS).

This species is named in honor of Dr. Gerrit Davidse, who was instrumental in establishing the "Flora Mesoamericana" project.

Syngonanthus davidsei is very similar to the four species endemic to Belize. Indeed, with the exception of *S. caulescens,* the Mesoamerican species are nearly identical in aspect and differ chiefly in the pubescence of the peduncle and in minor characters of the involucral bracts and sepals. Because of the great rarity of these six species (they are known from a total of only 12 collections), a proper assessment of the taxonomic value of their characters is premature at this time. In fact, since three of the Belize endemics (*S. hondurensis, S. lundellianus,* and *S. oniellii*) are known only from collections made by Hugh O'Niell in August and September 1936 within a few miles of Boomtown, it is tempting to consider these as belonging to a single, somewhat variable, species. It is therefore with some hesitation that I venture to describe a new species in this group. However, *S. davidsei* seems distinctive on the basis of its broadly ovate, blunt involucral bracts and its broadly ovate-falcate

staminate sepals, which are unlike those of any of the other Mesoamerican species.

Further collections of *Syngonanthus* from Mesoamerica are much to be desired in order to arrive at a proper taxonomic understanding of these species. For the time being, given the paucity of information available, recognition of these six species seems unavoidable.

Syngonanthus davidsei may be separated from its Mesoamerican congeners by means of the following key:

1a. Stems elongate; leaves arranged along stem (Veracruz, Costa Rica) ..... *S. caulescens* (Poir.) Ruhl.
1b. Stems very short, the plants essentially acaulescent; leaves tufted.
  2a. Peduncles glabrous, or nearly so.
    3a. Pistillate sepals glabrous; staminate corolla tube with petals free only at apex (Panama) ..... *S. pittieri* Mold.
    3b. Pistillate sepals long-ciliate on the margins; staminate petals connate at middle, free at base and at apex (Belize) ..... *S. oniellii* Mold.
  2b. Peduncles conspicuously pubescent.
    4a. Involucral bracts hyaline, colorless, the head white (Belize) ..... *S. bartlettii* Mold.
    4b. Involucral bracts golden brown or olivaceous.
      5a. Involucral bracts broadly ovate, obtuse to acute at apex; staminate sepals broadly obovate-falcate, obtuse to acute at apex, golden brown (Chiapas) ..... *S. davidsei* Huft
      5b. Involucral bracts lanceolate to narrowly elliptic or oblong, acute to acuminate at apex; staminate sepals elliptic, acuminate at apex (Belize).
        6a. Pubescence of peduncles strongly appressed, only a few spreading, glanduliferous hairs present ..... *S. hondurensis* Mold.
        6b. Pubescence of peduncles densely spreading glandular-pilose ..... *S. lundellianus* Mold.

I am grateful to Dr. Frank Almeda (CAS) for the loan of specimens and for information regarding the disposition of the isotypes.

—*Michael J. Huft, Missouri Botanical Garden. Mailing Address: Department of Botany, Field Museum of Natural History, Roosevelt Road at Lake Shore Drive, Chicago, Illinois 60605.*

BOOK REVIEW

Snijman, D. 1984. A revision of the genus *Haemanthus* L. (Amaryllidaceae). J. S. African Bot. Suppl. 12: 1–139.

Since the recognition of *Scadaxus* by Friis and Nordal in 1976, for tropical African species until then treated as *Haemanthus*, the genus has had a restricted application to species with true bulbs and somewhat fleshy distichous leaves. The genus as thus circumscribed is restricted to southern Africa where it has a wide range. This excellent revision by Dierdré Snijman of the Compton Herbarium, Kirstenbosch in Cape Town, is the only comprehensive treatment of the genus since "Flora Capensis" (1896) and admits 21 species of which four are new.

The study is the result of patient research over the several years needed to complete fieldwork and grow and flower the plants to observe the entire life cycle. *Haemanthus* presents the worker with an unusual problem: leaves of most species are produced after flowering. Thus populations found in flower must be revisited or grown to obtain leaf material, which in several cases is essential for species identification as well as for the preparation of type material. Conversely, plants collected in leaf had to be grown, sometimes for several years, before flowers could be obtained. The result of this labor is presented in a beautifully illustrated monograph that will be the envy of many a systematist. Twenty-four species and subspecies are illustrated with watercolors by Elaphie Ward-Hilhorst (and one is by Fay Anderson). The artwork and reproduction are of such quality that the plants come to life on the pages.

Haemanthus is concentrated in the winter rainfall area of southern Africa; which includes extreme southwestern Namibia, the south and west coasts, and interior of the Cape Province of South Africa. The pattern of speciation is one that is typical of many geophytic genera in southern Africa. There are a limited number of widespread and often morphologically variable species in the summer rainfall part of southern Africa. Then in contrast, there has been marked speciation in the south and west and many of the winter rainfall species are very restricted in distribution although well-known species such as *H. coccineus* and *H. pubescens* have wide ranges in this region.—*Peter Goldblatt, Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166.*

Volume 71, No. 2, pp. 344–630 of the ANNALS OF THE MISSOURI BOTANICAL GARDEN, was published on 19 March 1985.

Volume 71, No. 3, pp. 631–986 of the ANNALS OF THE MISSOURI BOTANICAL GARDEN, was published on 19 April 1985.

Volume 71, No. 4, pp. 987–1187 of the ANNALS OF THE MISSOURI BOTANICAL GARDEN, was published on 14 May 1985.

Volume 72, No. 1, pp. 1–166 of the ANNALS OF THE MISSOURI BOTANICAL GARDEN, was published on 10 June 1985.

Studies in *Fuchsia*

This special issue of the ANNALS OF THE MISSOURI BOTANICAL GARDEN (Vol. 69, no. 1, 1982) is devoted to several papers on the systematics of the genus *Fuchsia* (Onagraceae). The large section *Fuchsia*, which contains such horticulturally important species as *F. corymbiflora*, *F. triphylla*, and *F. fulgens*, contains 61 species, about 60% of the entire genus. Paul Berry's monograph treats the section in detail; extensive descriptions of flowers, blooming periods, habitats, and distribution are given. These are supplemented with beautiful color plates of several species. In addition to traditional keys to all the species, principal morphological differences between similar species and hybrids are treated in table form.

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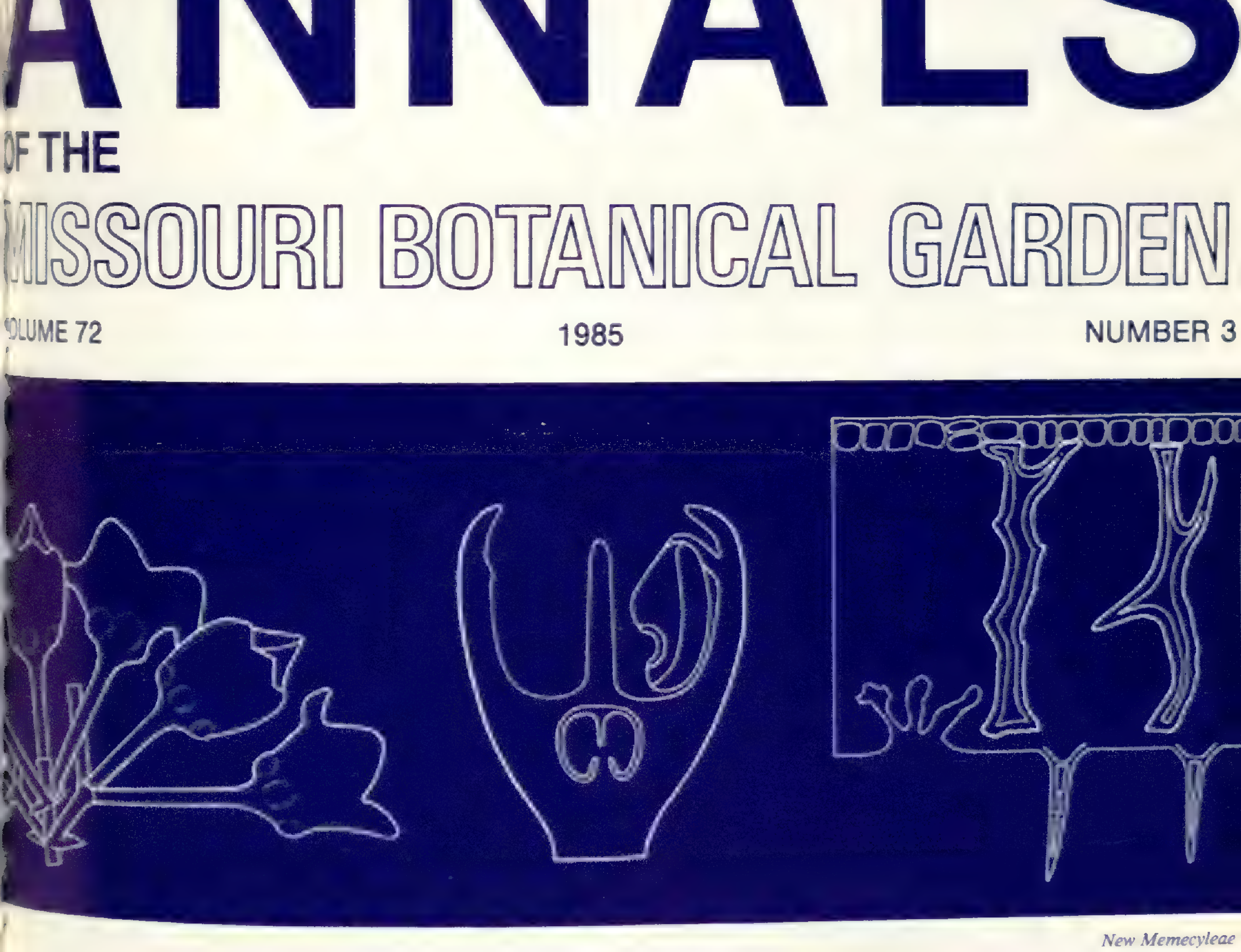

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THE HISTOGENESIS AND EVOLUTION OF INTEGUMENTS IN ONAGRACEAE[1]

HIROSHI TOBE[2] AND PETER H. RAVEN[3]

ABSTRACT

The mode of initiation and subsequent growth of the inner (i.i.) and outer (o.i.) integuments were examined and compared in 40 species, representing all seven tribes and all 17 genera of Onagraceae. The i.i. is of dermal origin and two-layered throughout the family. Four different types of developmental mode of the o.i. are characterized: 1) o.i. of subdermal origin—*Lopezia* (Lopezieae), *Fuchsia* (Fuchsieae), and *Circaea* (Circaeeae); 2) o.i. of both dermal and subdermal origin, with derivatives of the subdermal cells dividing more actively than those of the dermal cells—*Oenothera* and *Stenosiphon* (Onagreae); 3) o.i. of both dermal and subdermal origin, with derivatives of the subdermal cells dividing less actively than those of the dermal cells—*Hauya* (Hauyeae) and *Calylophus* and *Gaura* (Onagreae); 4) o.i. of dermal origin—*Ludwigia* (Jussiaeeae); *Boisduvalia* and *Epilobium* (Epilobieae); and *Camissonia, Clarkia, Gayophytum, Gongylocarpus, Heterogaura,* and *Xylonagra* (Onagreae). Except for the unexpected close similarity of *Hauya* (Hauyeae) to *Calylophus* and *Gaura* (Onagreae), among which is shared an apparently derived state of this character rather suggesting a common ancestry, the patterns of relationships suggested on the basis of the developmental mode of the o.i. closely accord with those derived from other lines of evidence. The results from Onagraceae confirm that the histogenetic characters of integuments are valuable indicators of relationship at a generic level.

The family Onagraceae, composed of seven tribes, 17 genera, and about 674 species (Raven, 1979), is one of the most intensively investigated families of angiosperms. In recent years, in addition to systematic studies (e.g., Raven, 1963, 1964, 1969; Plitmann et al., 1973), there have also been studies on chromosome number and morphology (e.g., Kurabayashi et al., 1962; Raven & Gregory, 1972; Raven & Tai, 1979), wood anatomy (Carlquist, 1975, 1977, 1982), pollen morphology (e.g., Skvarla et al., 1975, 1978), floral anatomy (Eyde & Morgan, 1973; Eyde, 1977, 1978, 1981, 1982), and leaf anatomy (Keating, 1982). As a result of these detailed studies, our knowledge of phylogenetic relationships within the family at a generic level has become quite detailed.

The major outlines of the pattern of relationships that have been revealed are as follows. *Ludwigia* represents a line distinct from all other genera of the family (Eyde, 1977, 1978, 1981; Raven & Tai, 1979). It shares with two of the more primitive genera in the other phylogenetic branch of the family, namely *Fuchsia* (Fuchsieae) and *Hauya* (Hauyeae), the generalized characteristic of lacking interxylary phloem (Carlquist, 1975, 1977). In addition to *Fuchsia* and *Hauya*, *Lopezia* (Lopezieae) and *Circaea* (Circaeeae), in

[1] We are grateful to the U.S. National Science Foundation for support of studies of Onagraceae through grants to Peter Raven, most recently grant BSR82-14879, and to Drs. F. Bouman and F. D. Boesewinkel for their critical reading of and comments on the manuscript.

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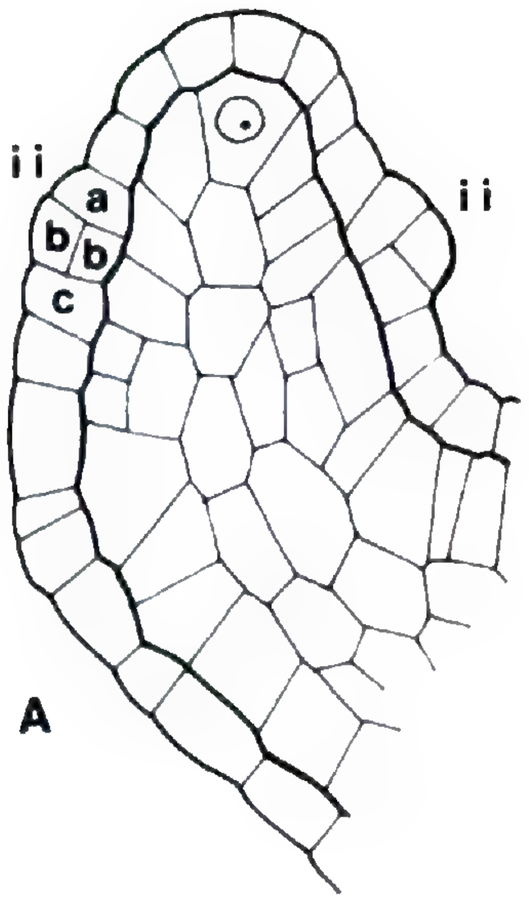
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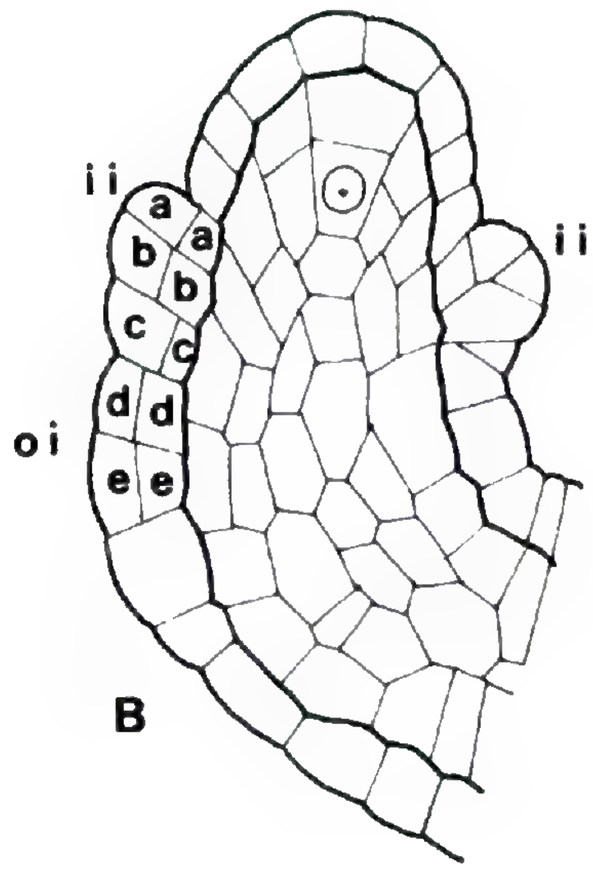
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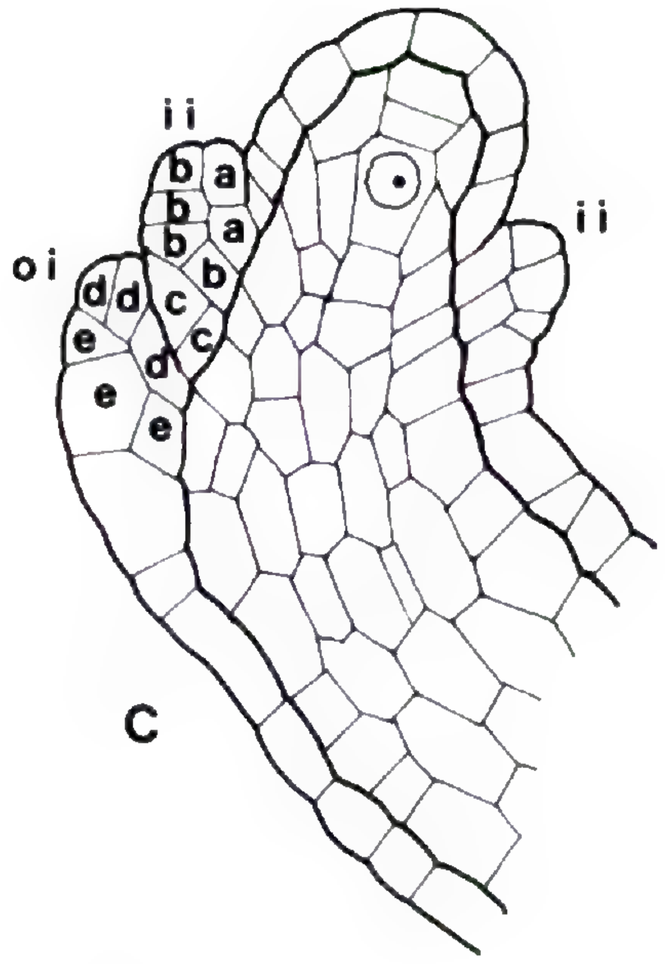
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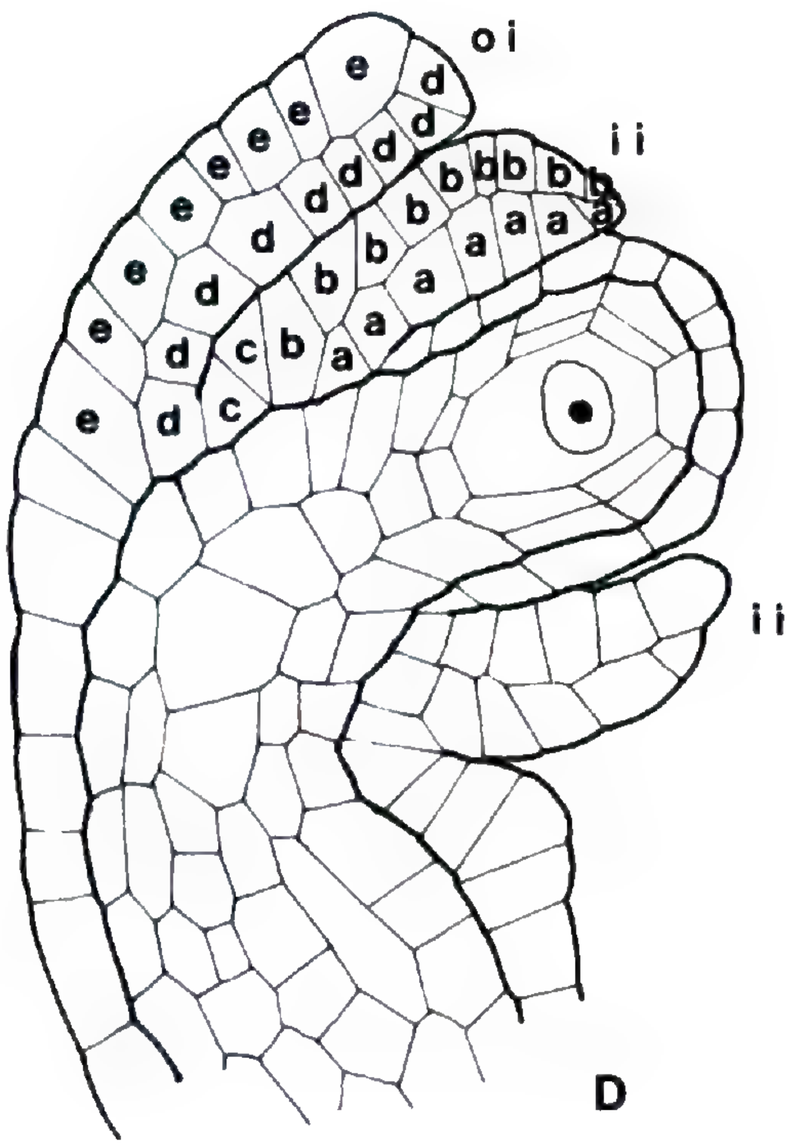
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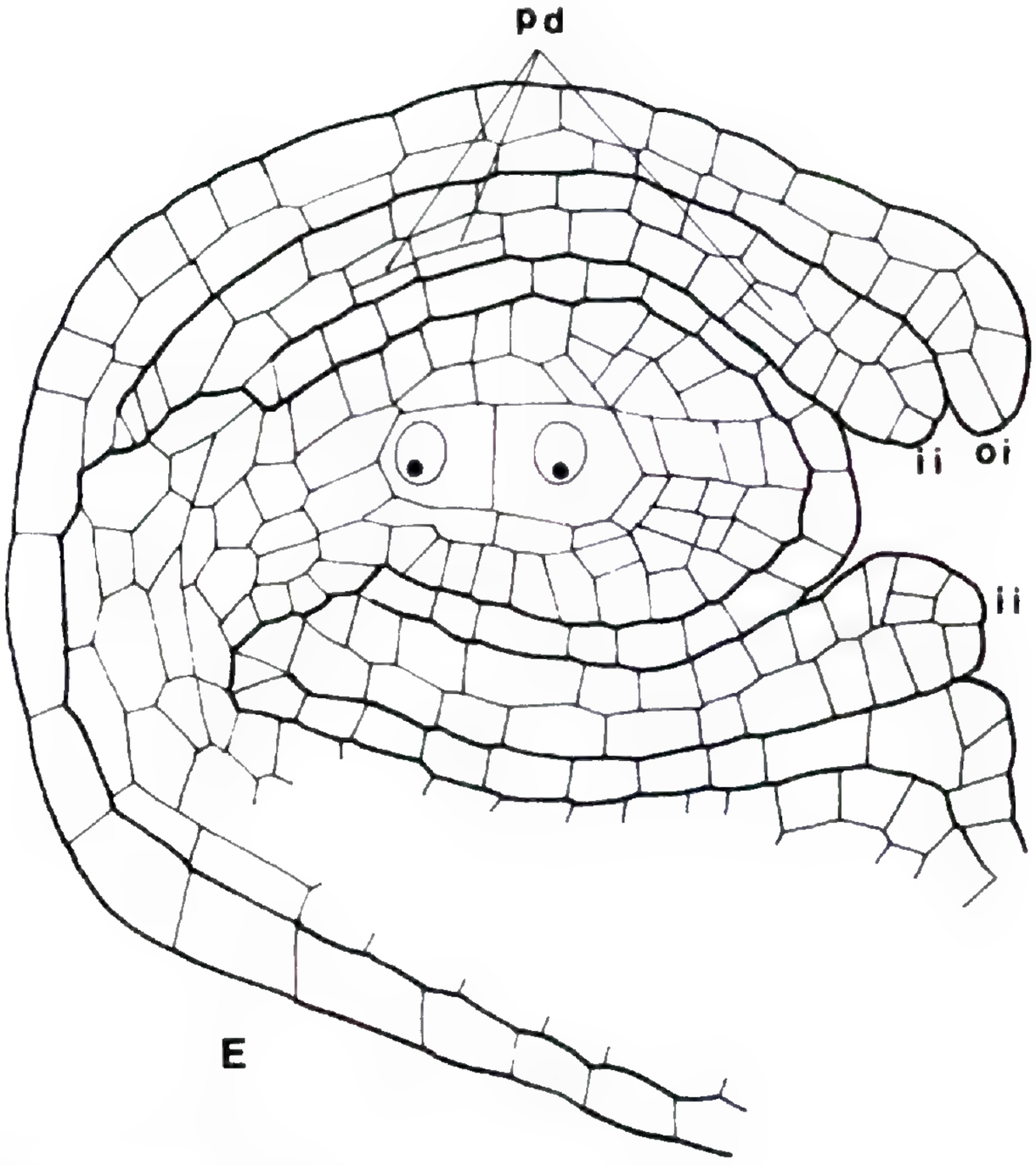
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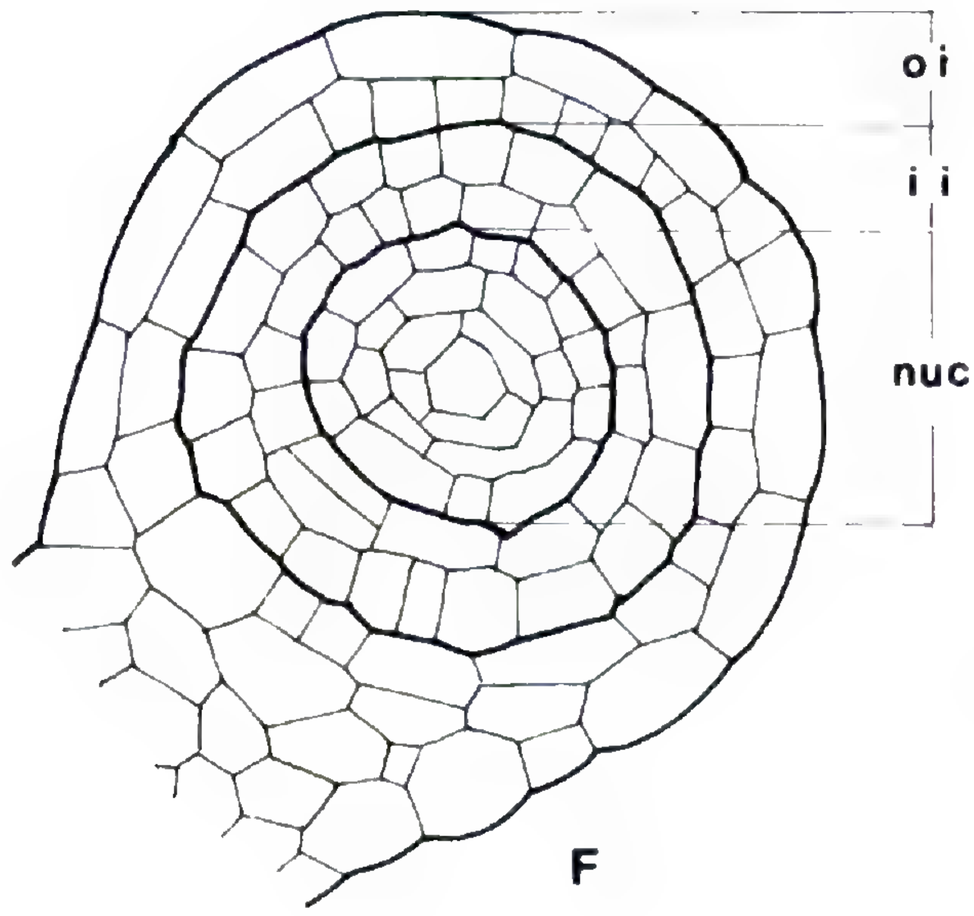
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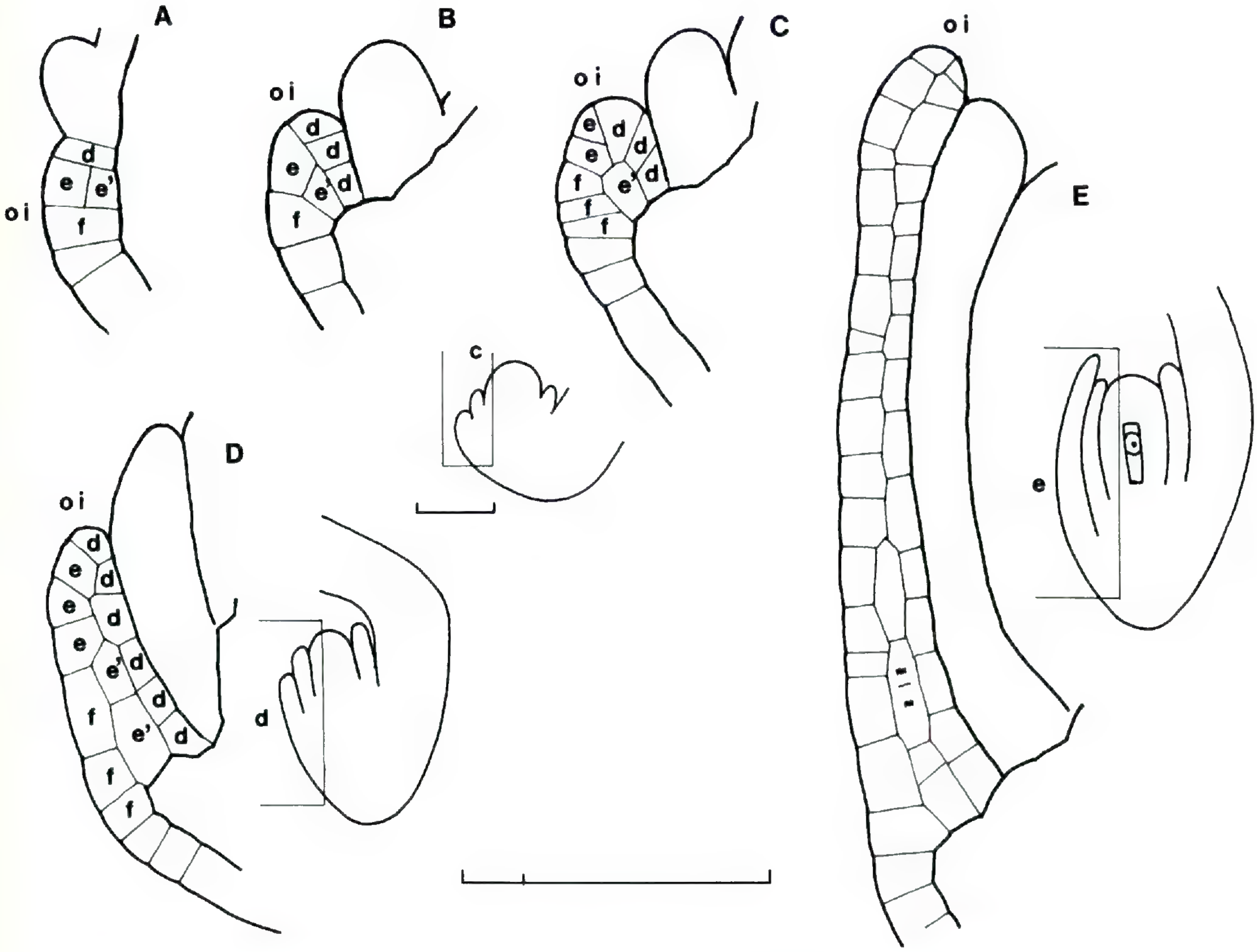

FIGURE 2. *Ludwigia peploides.*—A–E. Median longisections of the o.i. in progressively successive stages of development, showing the development of a distinctive three-layered part of the o.i. d, e, f, dermal initials of the o.i.; e', daughter cell of the dermal initial e, and functioning as an initial for the third (middle) layer of the o.i. Bracket scales = 100 μm.

which at least the most primitive species have a basic chromosome number of $n = 11$, present an array of relatively primitive characteristics, so that *Circaea, Fuchsia, Hauya,* and *Lopezia* may be regarded as distantly related, generalized lines within this major branch of the family—the branch that does *not* include *Ludwigia.* Epilobieae, consisting of *Boisduvalia* and *Epilobium* only, is advanced in many of its characteristics but occupies a rather isolated position within the family (Raven, 1976). Within the group of ten genera recognized as Onagreae (Raven, 1964, 1969), *Clarkia* and *Heterogaura* constitute one distinctive group; *Oenothera* and *Stenosiphon* another; *Calylophus* and *Gaura* a third; and *Camissonia, Gongylocarpus, Gayophytum,* and *Xylonagra* a fourth (Tobe & Raven, 1985). *Hauya* (Hauyeae) has been separated as a distinct tribe by virtue of its generalized characteristics including the presence of stipules, generalized leaf anatomy distinct from that of all Onagreae (Keating, 1982), and lack of interxylary phloem. On the other hand, its possession of obviously divided sporogenous tissue generally similar to

←

FIGURE 1. *Ludwigia arcuata.*—A–D. Median longisections of ovule primordia in progressively successive stages of development, showing that both the inner (i.i.) and outer (o.i.) integuments are of dermal origin. a, b, c, dermal initials of the i.i.; d, e, dermal initials of the o.i.—E. Median longisection of a growing ovule, in which periclinal cell divisions (pd) take place in the inner layer of the i.i.—F. Cross section of a growing ovule. nuc, nucellus. Bracket scale = 100 μm.

TABLE 1. A comparison of histogenetic characteristics of integuments in Onagraceae. Degree of participation of derivatives of subdermal initials in formation of the outer integument (o.i.) defined as follows: (+++) up to the tip of o.i. (see Fig. 10A); (++) more than half as much as, but less than, the whole length of o.i. (see Fig. 10B); (+) up to only the basal part of o.i. (see Fig. 10C); (−) no derivatives of subdermal initials contribute to the formation of o.i. (see Fig. 10D).

Taxon	Locality and Collection Information	Number of Cell Layers in Integument		Origin of Outer Integument	Degree of Participation of Derivatives of Subdermal Initials in Formation of Outer Integument
		Inner	Outer		
Tribe Jussiaeeae					
Ludwigia arcuata Walt.	U.S.A. Florida: Hillsborough Co., *Peng 4320* (MO).	2	2	dermal	−
L. bonariensis (Mich.) Hara	Argentina. Buenos Aires: La Plata, *Ramamoorthy 1005* (MO).	2	2	dermal	−
L. peploides (H.B.K.) Raven	U.S.A. Missouri: St. Louis Co., *Tobe,* 1981 (MO).	2	2–3	dermal	−
L. lanceolata Ell.	U.S.A. Georgia: McIntosh Co., *Peng 4139* (MO).	2	2	dermal	−
L. linearis Walt.	U.S.A. Louisiana: St. Tammany Parish, *Dille 420* (MO).	2	2	dermal	−
L. leptocarpa (Nutt.) Hara	Brazil. Bentos: Santa Catarina, *Ramamoorthy 1134* (MO).	2	2	dermal	−
L. virgata Michx.	U.S.A. Alabama: Mobile Co., *Tobe,* 1981 (MO).	2	2	dermal	−
L. peruviana (L.) Hara	Australia. Mascot (7 km S of Sydney), *Briggs 7143* (NSW).	2	2	dermal	−
L. latifolia (Benth.) Hara	Costa Rica. Puntarenas, *Raven 21575* (MO).	2	2	dermal	−
Tribe Lopezieae					
Lopezia langmaniae Miranda	Mexico. Chiapas, *Breedlove 32300* (CAS).	2	3–4	subdermal	+++
L. racemosa Cav. subsp. *racemosa*	Mexico. Chiapas, *Breedlove 7030* (CAS).	2	3–4	subdermal	+++
L. semeiandra Plitmann, Raven & Breedlove	Mexico. Sinaloa, *Breedlove 8044* (CAS).	2	3–4	subdermal	+++
Tribe Fuchsieae					
Fuchsia radicans Miers.	Brazil. São Paulo: Campas de Jordão, *Ramamoorthy 676* (MO).	2	3–6	subdermal	+++
F. jimenezii Breedlove, Berry & Raven	Costa Rica. Monteverde Preserve, *Haber, Baker & Baker 434* (MO).	2	3–4	subdermal	+++

TABLE 1. Continued.

Taxon	Locality and Collection Information	Number of Cell Layers in Integument		Origin of Outer Integument	Degree of Participation of Derivatives of Subdermal Initials in Formation of Outer Integument
		Inner	Outer		
F. microphylla H.B.K. subsp. *quercetorum* Breedlove	Cultivated, Univ. Calif. Bot. Gard. (Berkeley), *Raven,* 1969 (MO).	2	3–6	subdermal	+++
Tribe Circaeeae					
Circaea cordata Royle	Cultivated, Missouri Bot. Gard. #762431, original plants collected by Raven in 1975 from Vladivostok, USSR (MO).	2	3–5	subdermal	+++
C. alpina L. subsp. *pacifica* (Asch. & Mag.) Raven	Cultivated, Univ. British Columbia Bot. Gard. (UBC).	2	3–5	subdermal	+++
Tribe Hauyeae					
Hauya elegans DC. subsp. *elegans*	Mexico. Chiapas, *Breedlove 42631* (MO).	2	2–5	dermal and subdermal	+
H. heydeana Donn. Smith	Mexico. Chiapas: Ocotal Grande, *Breedlove 15669* (MO).	2	2–5	dermal and subdermal	+
Tribe Onagreae					
Gongylocarpus fruticulosus (Benth.) Raven & Breedlove	Mexico. Baja California: Magdalena Is., *Verity 037* (MO).	2	2	dermal	–
G. rubricaulis Schlecht. & Cham.	Mexico. Chiapas, *Breedlove 41880* (CAS).	2	2	dermal	–
Gayophytum humile Juss.	U.S.A. Oregon: Jefferson Co., *Chambers 4834* (OSC).	2	2	dermal	–
G. heterozygum Lewis & Szwey.	U.S.A. Oregon: Jefferson Co., *Chambers 4835* (OSC).	2	2	dermal	–
Xylonagra arborea (Kellogg) Donn. Smith & Rose	Mexico. Baja California, *Verity, Nakai & Angel,* 1979, no voucher.	2	2	dermal	–
Camissonia ovata (Nutt. ex Torr. & A. Gray) Raven	U.S.A. California: Marin Co., *Raven & Raven 26148* (MO).	2	2	dermal	–
C. californica (Nutt. ex Torr. & A. Gray) Raven	Cultivated, UCLA Bot. Gard., *Verity,* no voucher.	2	2	dermal	–

TABLE 1. Continued.

Taxon	Locality and Collection Information	Number of Cell Layers in Integument		Origin of Outer Integument	Degree of Participation of Derivatives of Subdermal Initials in Formation of Outer Integument
		Inner	Outer		
Calylophus lavandulifolius (Torr. & A. Gray) Raven	U.S.A. Nevada: Lincoln Co., *Tiehm & Williams 6572* (MO).	2	2–3	dermal and subdermal	+
C. serrulatus (Nutt.) Raven	U.S.A. Kansas: Sherman Co., *Brooks 15533* (KANU).	2	2–3	dermal and subdermal	+
Gaura coccinea Pursh	U.S.A. Texas: Pecos Co., *Powell 3589* (MO).	2	2–4	dermal and subdermal	+
G. longiflora Spach	U.S.A. Missouri: Jefferson Co., *Wagner, Mill & Tobe 4522* (MO).	2	2–3	dermal and subdermal	+
Oenothera flava (A. Nels.) Garrett subsp. *flava*	Mexico. Durango, *Wagner & Solomon 4321* (MO).	2	2–5	dermal and subdermal	++
O. villosa Thunb. subsp. *villosa*	U.S.A. Missouri: St. Louis Co., *Wagner, Chin & Tobe 4519* (MO).	2	2–5	dermal and subdermal	++
Stenosiphon linifolius (Nutt.) Heynh.	U.S.A. Oklahoma: McClain Co., *Sullivan 1038* (OKL).	2	2–4	dermal and subdermal	++
Clarkia delicata (Abrams) Nels. & Macbr.	Mexico. Baja California, *Moran 27640* (MO).	2	2	dermal	–
C. tenella (Cav.) Lewis subsp. *tenella*	Chile. Malleco: Curacao, *Marticorena & Ovezada 1669* (MO).	2	2	dermal	–
Heterogaura heterandra (Torr.) Coville	U.S.A. California: Tuolumne Co., *Gottlieb,* 1977 (MO).	2	2	dermal	–
Tribe Epilobieae					
Boisduvalia subulata (Ruiz. & Pavón) Raimann	Chile. Ñuble, *Cheese & Watson 4405* (K).	2	2	dermal	–
B. glabella (Nutt.) Walp.	U.S.A. California: Yolo Co., *Crampton 9212* (MO).	2	2	dermal	–
Epilobium ciliatum Raf. subsp. *watsonii* (Barbey) Hoch & Raven	U.S.A. California: Marin Co., *Sharp,* 1967 (MO).	2	2	dermal	–
E. canum (Greene) Raven subsp. *canum*	Cultivated, Univ. Calif. Bot. Gard. (Berkeley) UCBG 58.996 (UC).	2	2	dermal	–

that found in *Calylophus, Clarkia, Gaura,* and *Heterogaura,* has been used as evidence for linking it with these groups (Raven, 1964, 1969, 1979), as have its vespertine flowers, long floral tubes, white petals, and strong floral odor, this syndrome of characteristics closely resembling that found in white-flowered species of *Oenothera.*

The histogenesis of integuments which is the subject of this paper is used here as another approach to clarify the relationships between the genera of Onagraceae. Although such characteristics have traditionally been included within the scope of investigations of embryologists, they have largely been confined to considerations of the number and thickness of the integuments, the development of integuments into seed coats, and the participation of integuments in formation of the micropyle. In contrast, little attention has been devoted to the developmental mode of the outer and inner integuments (see reviews in Bouman, 1971, 1974, 1984). Twenty-five years ago, the studies of Roth (1957) on *Capsella* began to interest embryologists again in the developmental mode of integuments, a field that had been largely neglected since the studies of Warming (1878) over a century ago. The subsequent works of Bouman and his collaborators on *Juglans* and *Pterocarya* (Boesewinkel & Bouman, 1967), on Polycarpicae (Bouman, 1971, 1977, 1978; Boer & Bouman, 1972, 1974), and on Rutaceae (Boesewinkel, 1977, 1978; Boesewinkel & Bouman, 1978) have increasingly called our attention to the histogenetic characters of integuments as a probable indicator of affinity among taxa. Bouman (1971) emphasized the importance of observations of the histogenesis of integuments in their evaluation, citing the fact that seemingly identical structure of integuments often developed as a result of different histogenetic processes. He also warned against the taxonomic value of data based on the structure of the mature seed coat for similar reasons. For example, *Drimys winteri* Forst. (Winteraceae) has an outer integument of dermal origin (Boer & Bouman, 1974), whereas *Magnolia stellata* (Sieb. & Zucc.) Maxim., *M. virginiana* L., and *Liriodendron tulipifera* L. (Magnoliaceae) have an outer integument of subdermal origin (Boer & Bouman, 1972; Bouman, 1977). This difference in the histogenetic origin of the outer integument has been used as additional evidence for separating Winteraceae from Magnoliaceae, with which they were combined earlier (Boer & Bouman, 1974).

We have made observations of the histogenesis of the integuments as part of a study of the embryology of Onagraceae. In this paper we shall deal only with the mode of initiation and subsequent growth of the integuments, not considering the more diversified morphology of the seed coat or testa. We shall utilize the mode of initiation and subsequent growth of integuments solely as an indicator of affinity between taxa and shall attempt neither morphological interpretations of these structures nor detailed studies of other aspects of embryology in these plants.

Only one earlier paper deals with the histogenesis of integuments of Onagraceae (Geerts, 1908). Geerts provides excellent illustrations of the young ovules of *Oenothera glazioviana* Mich. (= "*O. lamarckiana*"), stating "Das innere Integument entwickelt sich nur aus Dermatogenzellen, zur Bildung des äusseren Integumentes finden im Periblem Teilungen statt." Several other papers dealing with the embryology of Onagraceae (e.g., O'Neal, 1923, *Oenothera biennis* L. = "*O. rubrinervis*"; Johansen, 1934, *Circaea alpina* subsp. *pacifica* = "*C. pacifica*"; Täckholm, 1914, *Lopezia racemosa* subsp. *racemosa* = "*L. coronata*") have illustrations of sections of young ovules including views of developing integuments; all of these papers, however, lack an explanation of the histogenesis of the structures illustrated and are not detailed enough to be used in connection with this present comparative study.

Materials and Methods

Forty species representing all seven tribes and all 17 genera of Onagraceae were included in our study. They are listed in Table 1, along with the results obtained from each. All the samples were fixed in FAA (90 parts 50 or 70% ethanol, 5 parts acetic acid and 5 parts formalin) and then dehydrated through tertiary-butyl alcohol series and embedded in paraplast. Serial microtome sections of ovaries 5–7 μm thick were stained with Heidenhain's hematoxylin, safranin, and fast green FCF.

In all Onagraceae, the ovule has two integuments, inner (i.i.) and outer (o.i.); it becomes anatropous or hemitropous (*Lopezia*) at maturity. The terminology, abbreviation of terms, and the manner of drawing microtome sections basically follow Bouman (1974). In every diagram illustrating the histogenesis of integuments, Figures 1, 2, 4–8 for example, bold lines are used

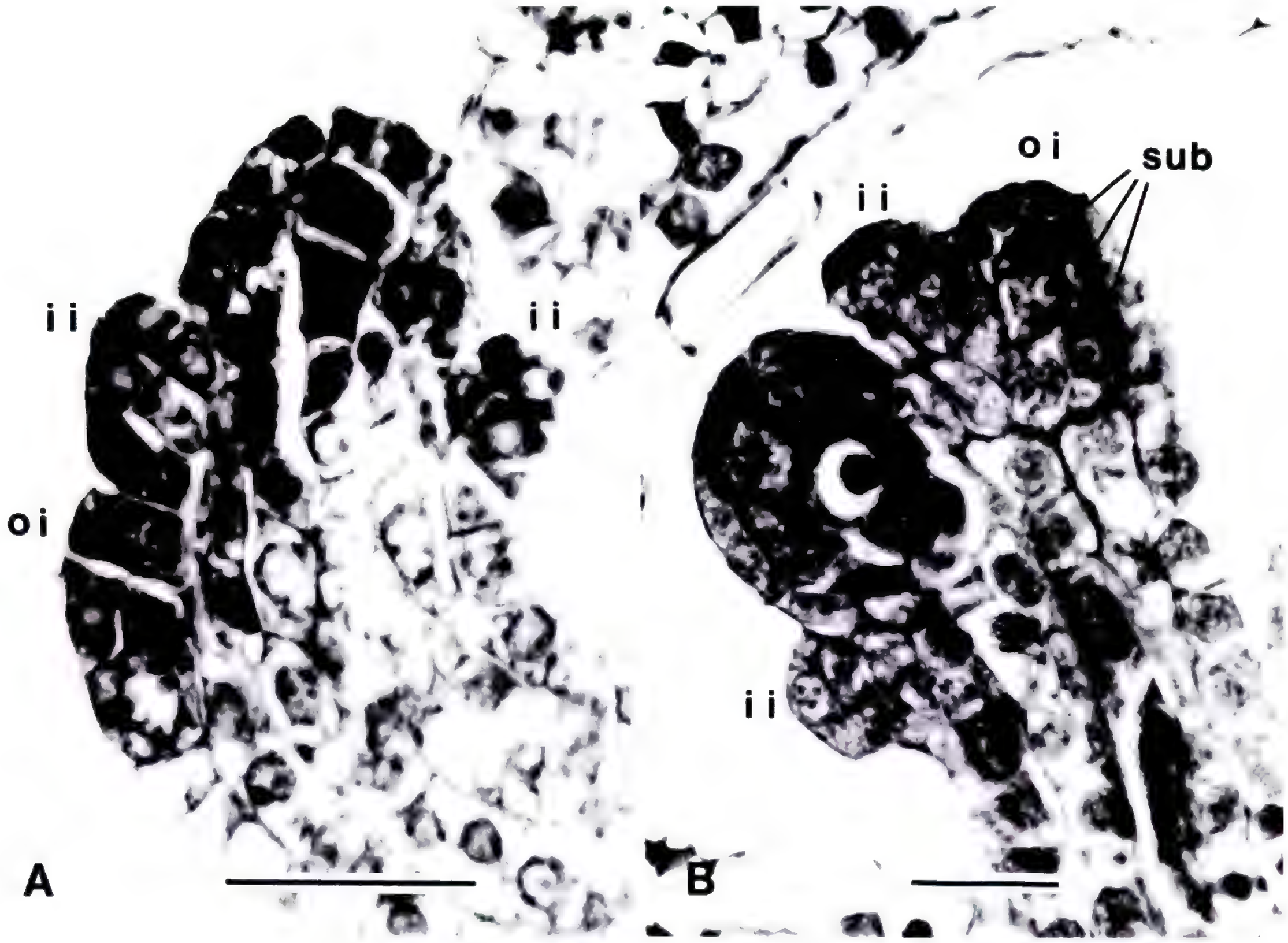

FIGURE 3. Median longisections of the ovule primordia, showing two contrasting developmental modes of the o.i.—A. *Ludwigia arcuata*. Note that the o.i. is initiated dermally.—B. *Lopezia racemosa*. Note that the o.i. is initiated subdermally. Scales = 20 μm.

to represent the boundary between dermal and subdermal tissues.

OBSERVATIONS

TRIBE JUSSIAEEAE

Ludwigia arcuata, L. bonariensis, L. latifolia, L. leptocarpa, L. linearis, L. peploides, L. peruviana, and *L. virgata*—In every species the initiation of the i.i. commences by periclinal divisions of dermal cells located at the flank of an ovule primordium (Fig. 1A, see cells b). In median longisections of the ovule primordium, three dermal initial cells (a, b, c in Fig. 1B; see also Fig. 3A), or occasionally only two, a and b, were recognized. The first periclinal divisions of these three initials form a swelling of the i.i., first discernible externally. The subsequent growth of the i.i. primordium takes place chiefly by divisions of daughter cells of two, a and b, initials (Fig. 1C, D), so that the i.i. grows as a two-layered thin organ. In a developed ovule the i.i. usually becomes three-layered because of periclinal divisions of cells of the inner layer of the i.i. (Fig. 1E, F). The tip of the i.i. ultimately becomes multilayered, forming an endostome similar to that known in many other angiosperms.

Thus, since the initiation and the subsequent growth of the i.i. takes place by divisions of dermal initials and their derivatives, the i.i. of *Lud-*

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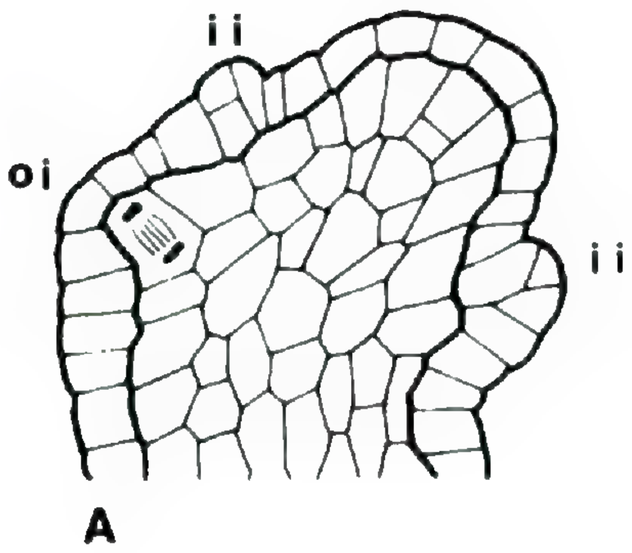
FIGURE 4. *Lopezia semeiandra.*—A–C. Median longisections of ovule primordia in progressively successive stages of development, showing that the i.i. is of dermal origin but the o.i. of subdermal origin.—D. Median longisections of a growing ovule.—E. Longisection of a lateral part of a developed ovule.—F. Longisection of a micropylar part of a developed ovule. Note that the derivatives of the subdermal initials reach up to the tip of the o.i. Bracket scales = 100 μm.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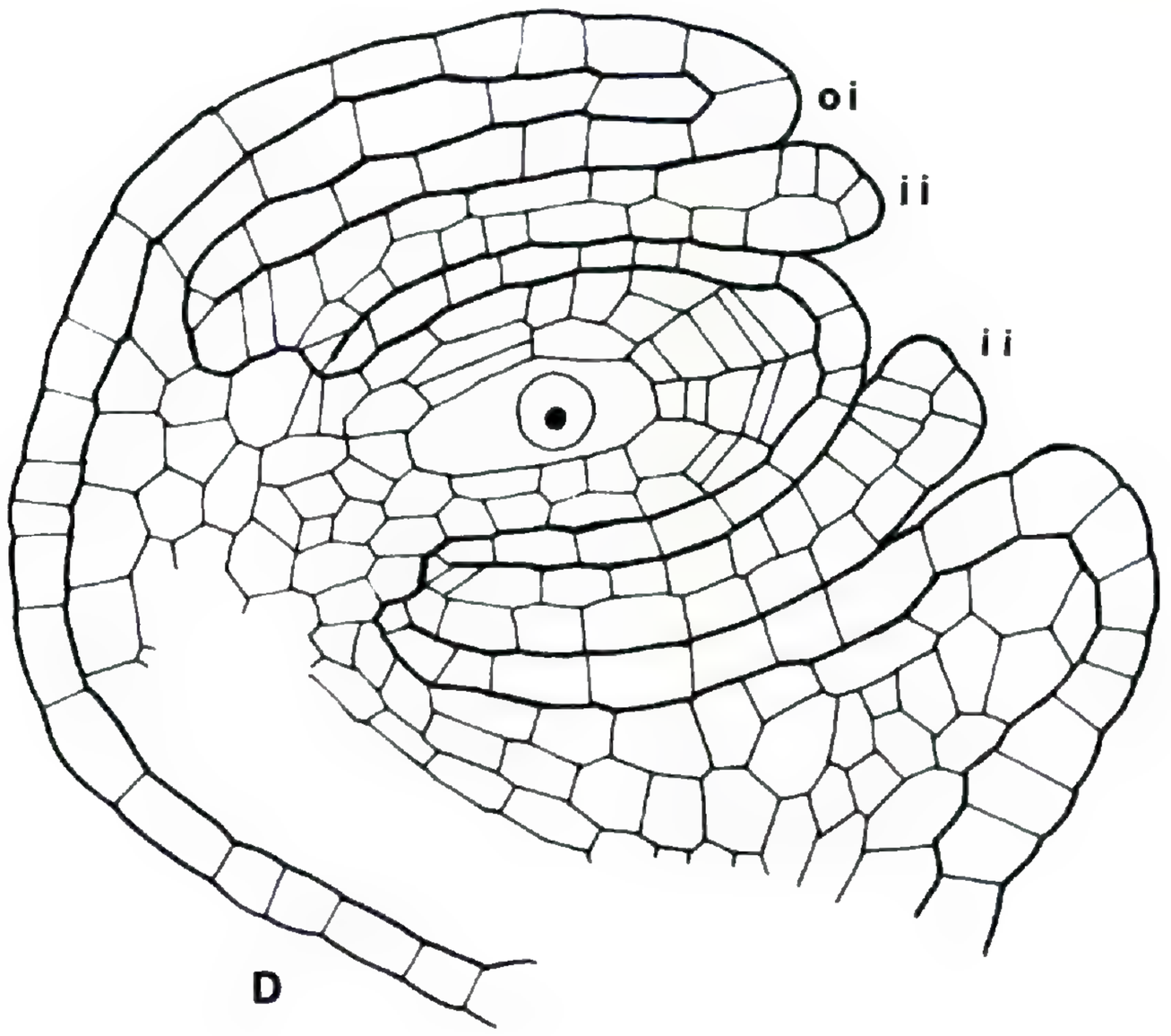
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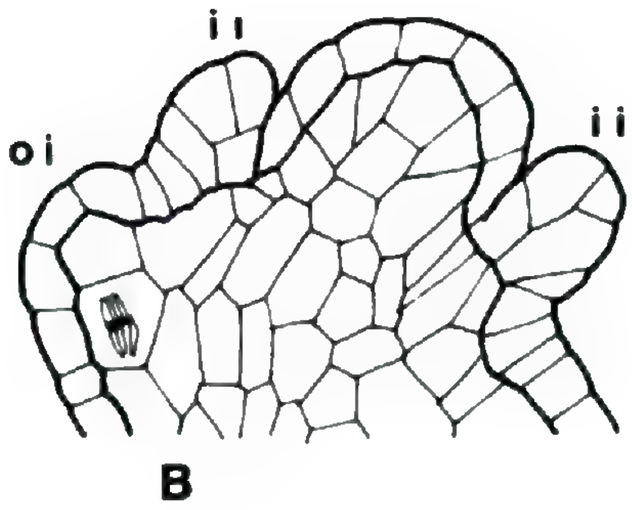
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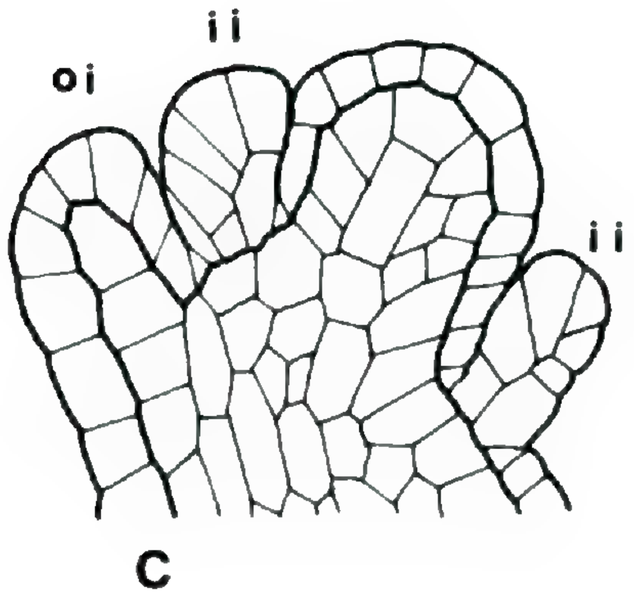
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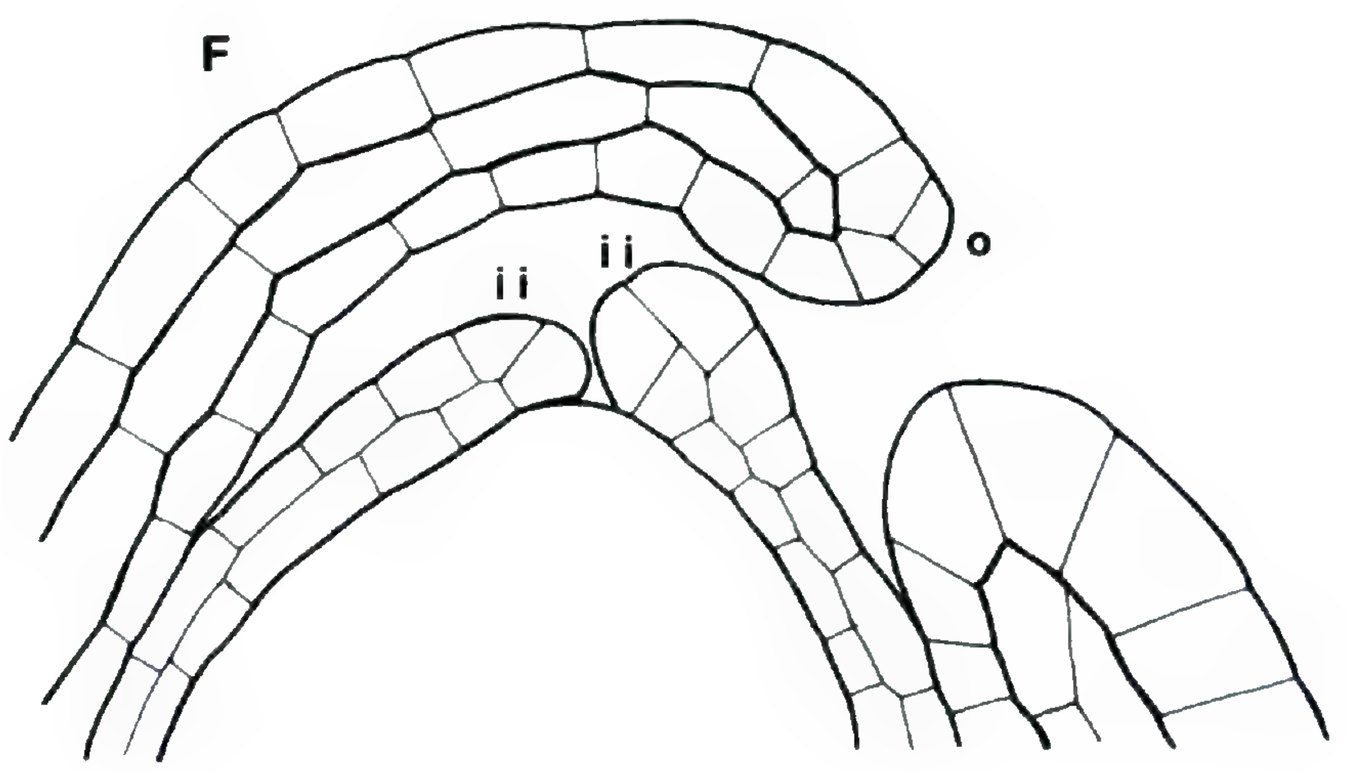
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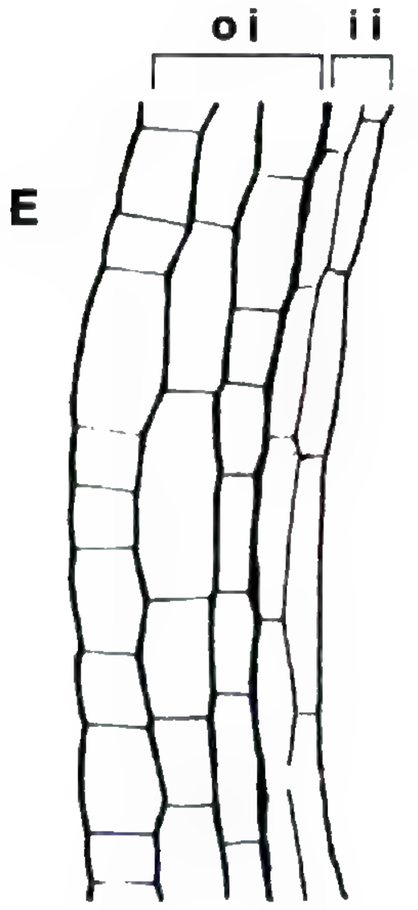
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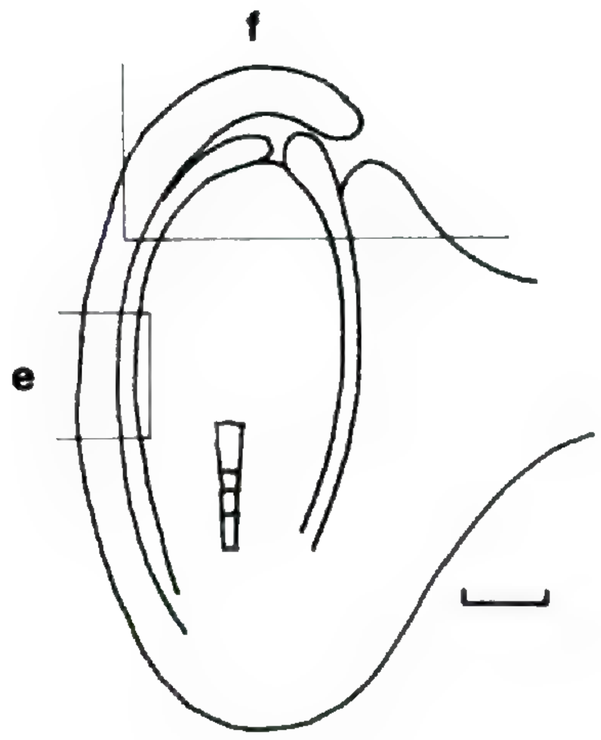
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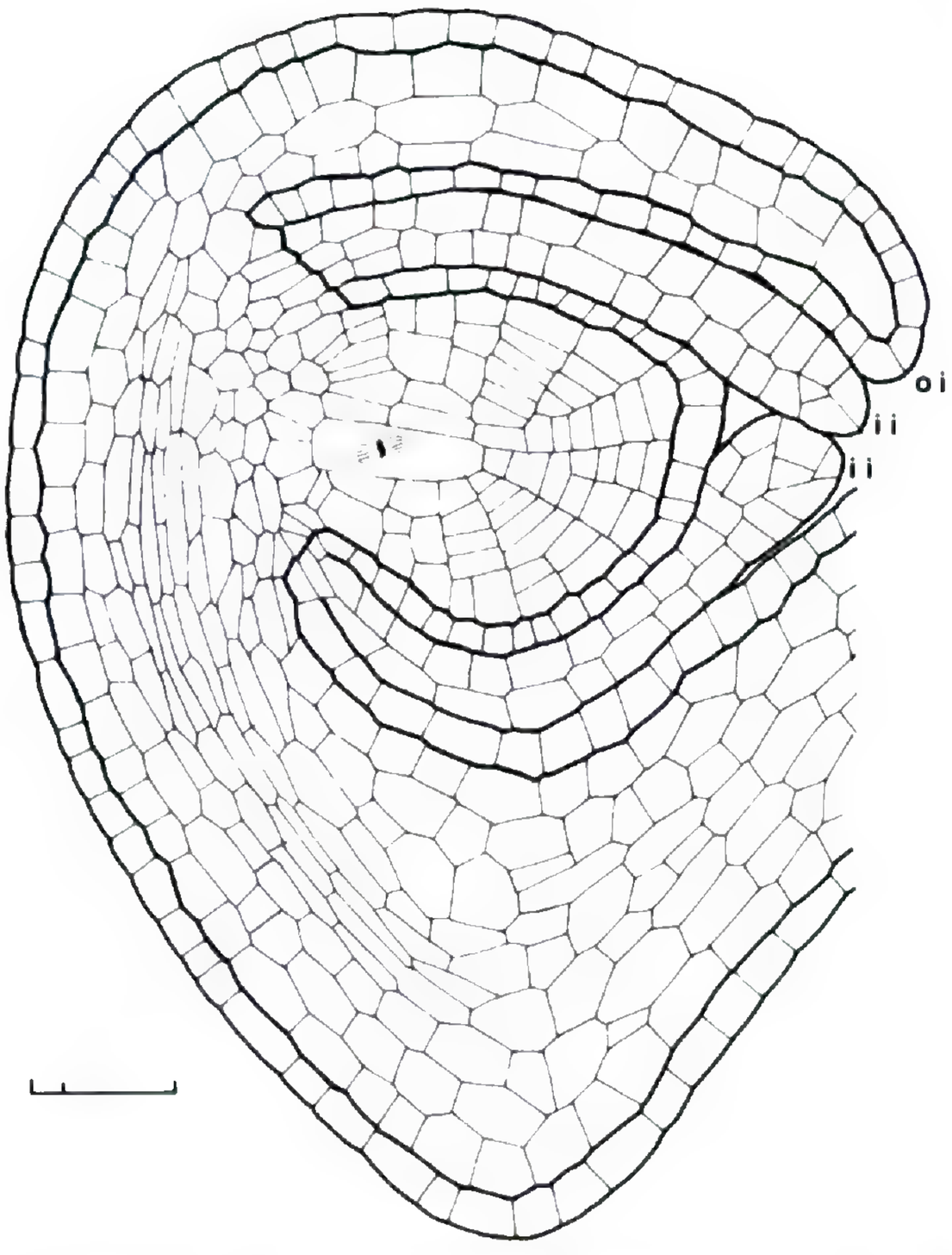


FIGURE 5. *Fuchsia radicans*. Note that the o.i. is of subdermal origin and the derivatives of the subdermal initials reach up to the tip of the o.i. Bracket scale = 100 μm.

wigia is of dermal origin, a term used consistently by Bouman and his collaborators to express this pattern of development.

The o.i. is also of dermal origin in all species examined. At the initiation stage, two dermal initials (d, e in Fig. 1B; see also Fig. 3A) undergo periclinal divisions. Subsequent growth takes place by repeated divisions of derivatives of the dermal initials (Fig. 1C, D). The mature o.i. is two-layered in all the species except *L. peploides* (Fig. 1E, F), and only its tip becomes multilayered to form an exostome. The o.i. hardly develops at the funicular side, and, if it does, it is made up on this side of derivatives of dermal initials only (Fig. 1E).

In the sole exceptional species, *L. peploides*, a developed o.i. is two-layered in the upper part and three-layered in the lower part (Fig. 2E). This three-layered part of the o.i. is formed in a different mode from that of the i.i. The first periclinal division of the dermal initial e gives rise to two daughter cells, the lower cell e′ functioning as a distinct initial of the third (middle) layer in the subsequent growth (Fig. 2A, B). Consequently, the upper part of the o.i. grows by divisions of the upper daughter cell e as well as of another initial d, and the lower part by divisions of derivatives of an additional initial f as well as of e′ and d (Fig. 2C, D).

TRIBE LOPEZIEAE

Lopezia langmaniae, L. racemosa and *L. semeiandra*—The i.i. is of dermal origin and two-layered in all species examined (Fig. 4A–F).

The mode of initiation and the subsequent growth of the o.i. is consistent in all species examined, differing completely from the pattern seen in *Ludwigia*. On the antiraphial and lateral sides, the initiation of the o.i. commences by periclinal divisions of subdermal cells, and not by those of dermal cells (Fig. 4A). Repeated periclinal divisions of subdermal cells give rise to a primordium of the o.i. discernible externally as a swelling (Fig. 4B, C; see also Fig. 3B). Subsequent growth proceeds by divisions of both subdermal and dermal cells (Fig. 4D). Thus, even if dermal cells will have divided periclinally to make an exostome at the tip of the o.i., derivatives of the subdermal initials reach the tip on all antiraphial and lateral sides (Fig. 4F). The mature o.i. is usually three-layered in the upper part and three- to four-layered in the lower part (Fig. 4E, F). In *Lopezia*, the mature ovule is hemianatropous, and therefore the o.i. is well developed on the funicular side also (Fig. 4D).

Thus, since subdermal initials and their derivatives contribute to the formation of the integument, the o.i. of *Lopezia* is of subdermal origin, a term used to express a mode contrasting with that in *Ludwigia*.

TRIBE FUCHSIEAE

Fuchsia jimenezii, F. microphylla subsp. *quercetorum*, and *F. radicans*—The i.i. is of dermal origin and two-layered in all species examined.

The o.i. is of subdermal origin in all species examined. Derivatives of subdermal initials participate in the formation of a major part of the o.i., and reach its apex as in *Lopezia* (Fig. 5). The thickness of the o.i. differs from species to species: three- to four-layered in *F. jimenezii*, and three- to six-layered in *F. radicans* (Fig. 5) and *F. microphylla*.

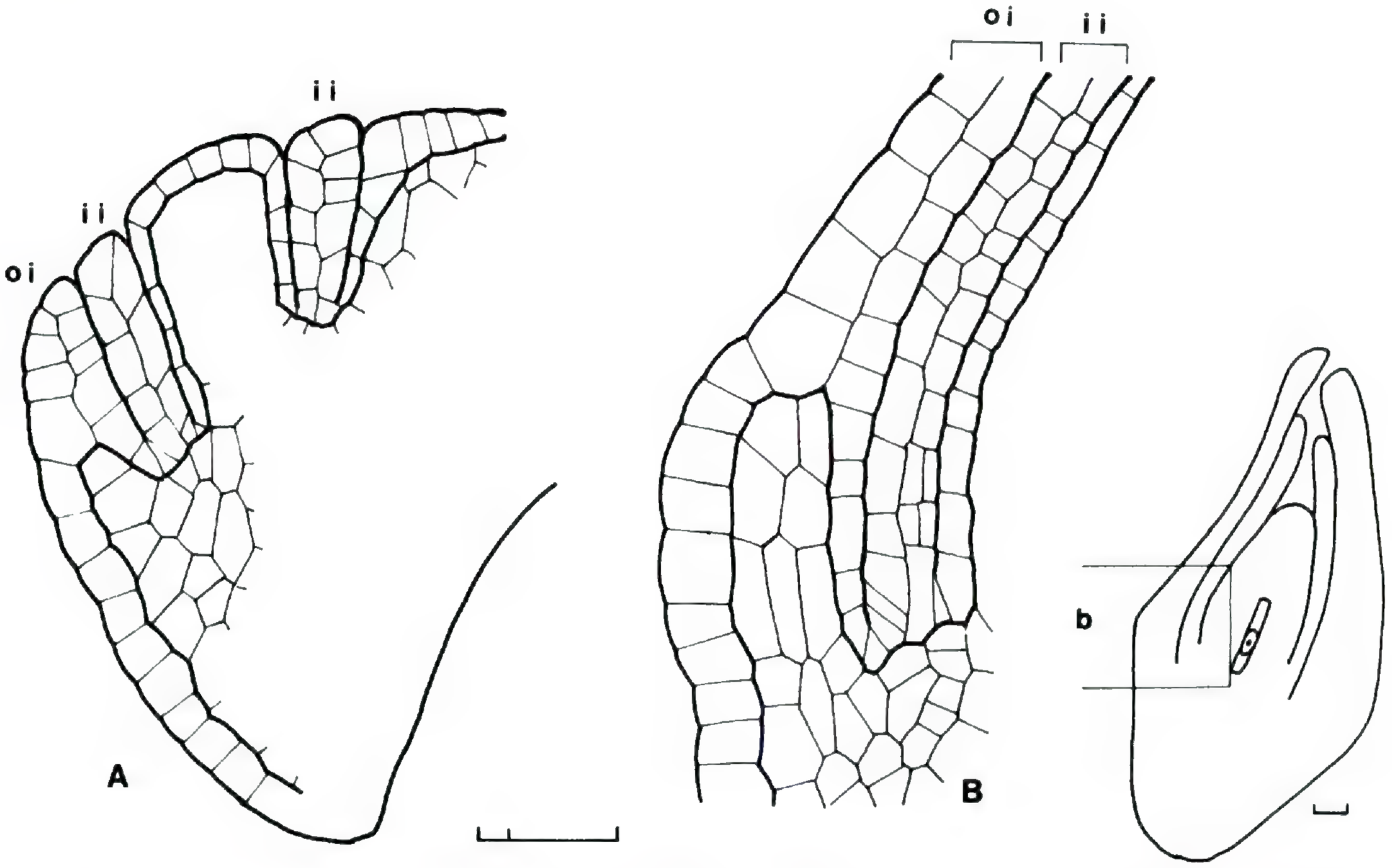


FIGURE 6. *Hauya elegans* subsp. *elegans*.—A. Median longisection of an ovule primordium.—B. Longisection of a developed ovule. Note that the o.i. is of both dermal and subdermal origin, and the derivatives of the dermal initials divide more actively than those of the subdermal ones in the formation of the o.i. Bracket scales = 100 μm.

TRIBE CIRCAEEAE

Circaea alpina subsp. *pacifica* and *C. cordata*—The i.i. is of dermal origin and two-layered in both species.

The o.i. is of subdermal origin and three- to five-layered in both species. Derivatives of subdermal initials reach the tip of the o.i. as in *Lopezia* and *Fuchsia* (Fig. 9A).

TRIBE HAUYEAE

Hauya elegans subsp. *elegans* and *H. heydeana*—The i.i. is of dermal origin and two-layered in both species (Fig. 6A, B).

The o.i. is of both dermal and subdermal origin in both species. On the antiraphial and lateral surfaces, the initiation of the o.i. commences with periclinal divisions of dermal as well as of subdermal initials (Fig. 6A). Subsequently, however, derivatives of the dermal initials divide more actively than those of the subdermal initials, so that the derivatives of the subdermal initials remain in the basal part of the o.i. on the antiraphial and lateral sides (Fig. 6B). Consequently, the mature o.i. is mostly two-layered, but three- to five-layered in its basal portion in both species (Fig. 6B).

TRIBE ONAGREAE

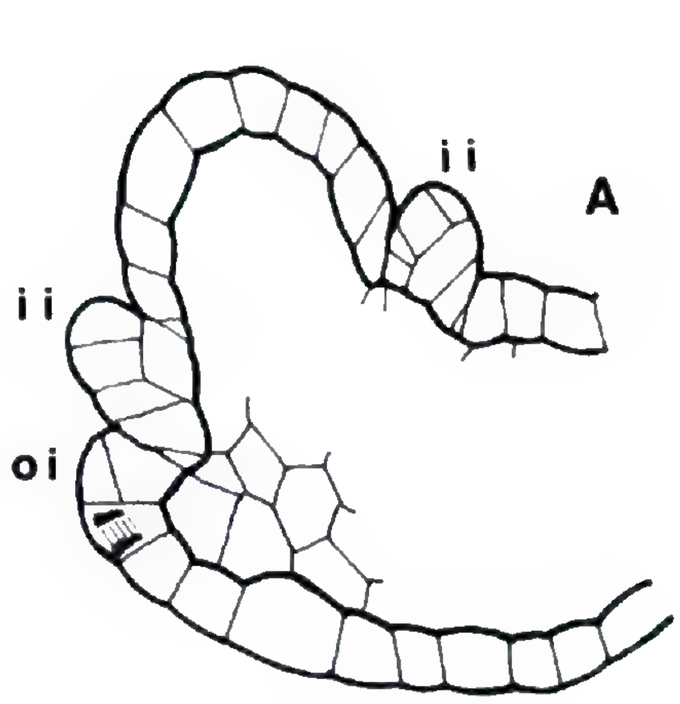
Gongylocarpus fruticulosus and *G. rubricaulis*—Both the i.i. and the o.i. are of dermal origin and two-layered in both species.

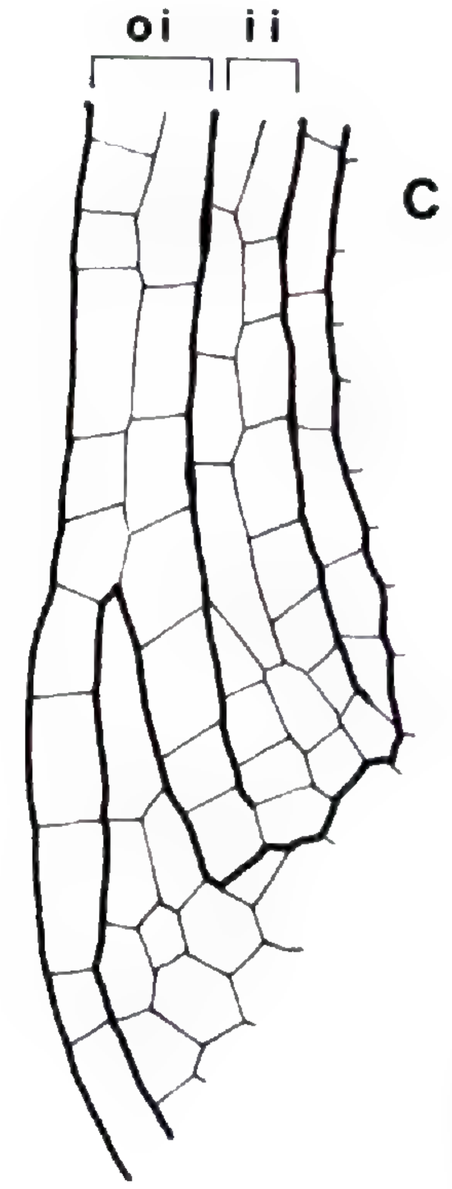
Gayophytum heterozygum and *G. humile*—Both the i.i. and the o.i. are of dermal origin and two-layered in both species.

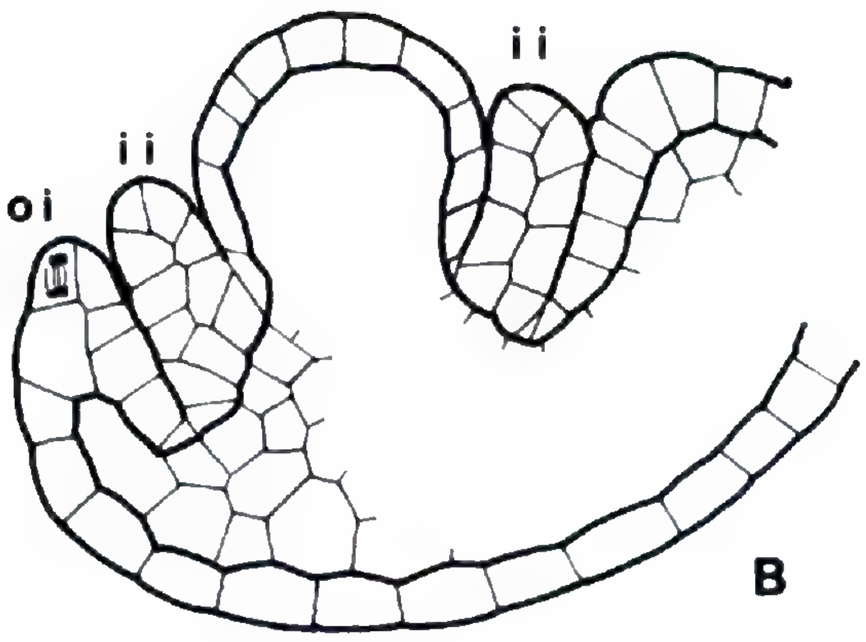
Xylonagra arborea—Both the i.i. and the o.i. are of dermal origin and two-layered.

Camissonia californica and *C. ovata*—Both the i.i. and the o.i. are of dermal origin and two-layered in both species.

Calylophus lavandulifolius and *C. serrulatus*—The i.i. is of dermal origin and two-layered in both species. The mode of the initiation and the subsequent growth of the o.i. is similar to that in *Hauya*. In both species the o.i. is initiated by periclinal divisions of dermal as well as of subdermal initials (Fig. 7A). Derivatives of the dermal initials divide more often than those of the subdermal initials subsequently (Fig. 7B). Ultimately, the derivatives of subdermal initials par-







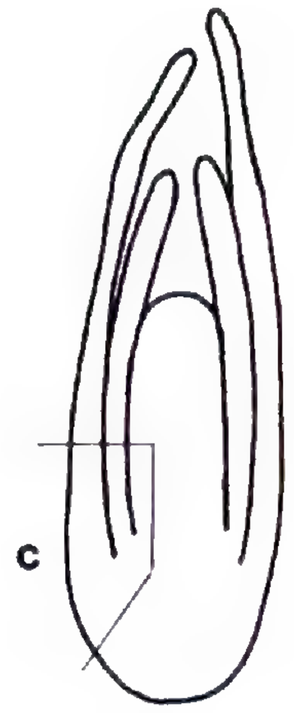


FIGURE 7. *Calylophus lavandulifolius*.—A, B. Median longisections of ovule primordia in progressively successive stages of development, showing that the o.i. is of both dermal and subdermal origin.—C. Longisection of a developed ovule. Note that the derivatives of the dermal initials divide more often than those of the subdermal ones in the formation of the o.i. Bracket scales = 100 μm.

ticipate only in the formation of the basal part of the o.i. (Fig. 7C). The mature o.i. is mostly two-layered but three- to four-layered in its basal portion (Fig. 7C).

Gaura coccinea and *G. longiflora*—The i.i. is of dermal origin and two-layered, and the o.i. of both dermal and subdermal origin in both species. The degree of participation of derivatives of subdermal initials in the formation of the o.i. closely resembles that seen in *Hauya* and *Calylophus*. Therefore, the mature o.i. is mostly two-layered but three- to four-layered in its basal portion, which is made up of derivatives of dermal and subdermal initials.

Oenothera flava subsp. *flava* and *O. villosa* subsp. *villosa*—The i.i. is of dermal origin, as Geerts (1908) observed, and two-layered in both species. On the antiraphial and lateral sides, the o.i. is of both dermal and subdermal origin in both species. Geerts (1908) mentioned that in *O. glazioviana* (= "*O. lamarckiana*"), the o.i. is produced by divisions of subdermal cells. But his figure (Geerts, 1908, table 19, fig. 3) illustrating a median longisection of the very young ovule primordium shows the o.i. swelling by divisions of derivatives of both dermal and subdermal initials. In both species examined in this paper, the dermal and the subdermal initials appear to divide almost simultaneously (Fig. 8A). In any event, at least it is obvious that the derivatives of both the dermal and subdermal initials contribute to the formation of the o.i. Of more importance to the final outcome is the fact that the derivatives of the dermal initials divide less actively than those of the subdermal ones, a feature in which *Oenothera* differs from *Hauya, Calylophus,* and *Gaura* (Fig. 8B). The mature o.i. is two-layered in the upper portion and three-layered in the lower portion (Fig. 8C).

Stenosiphon linifolius—The i.i. is of dermal origin and two-layered. The mode of initiation and the subsequent growth of the o.i. is almost identical to that in *Oenothera*. On the antiraphial and lateral sides, the o.i. is of both dermal and

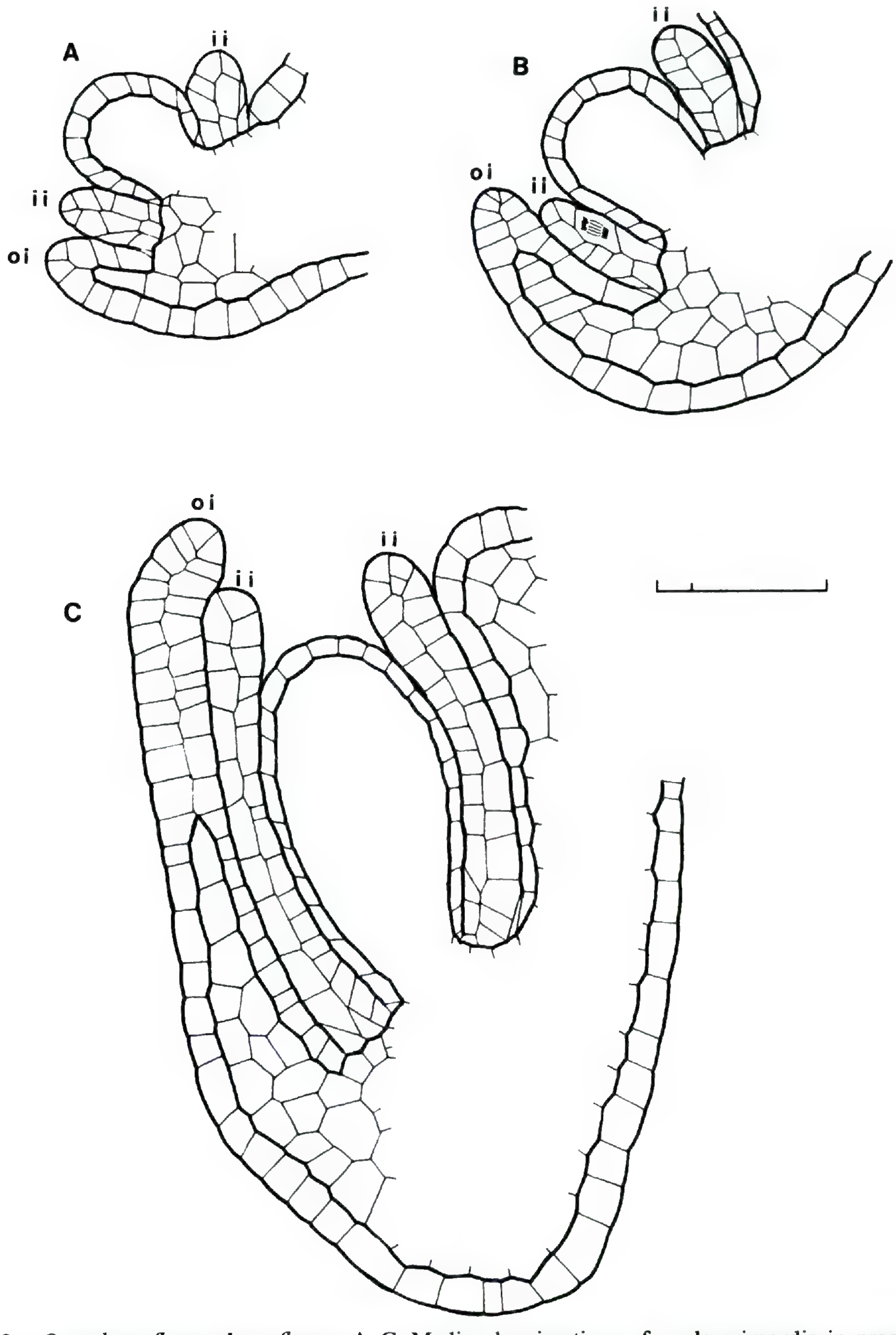
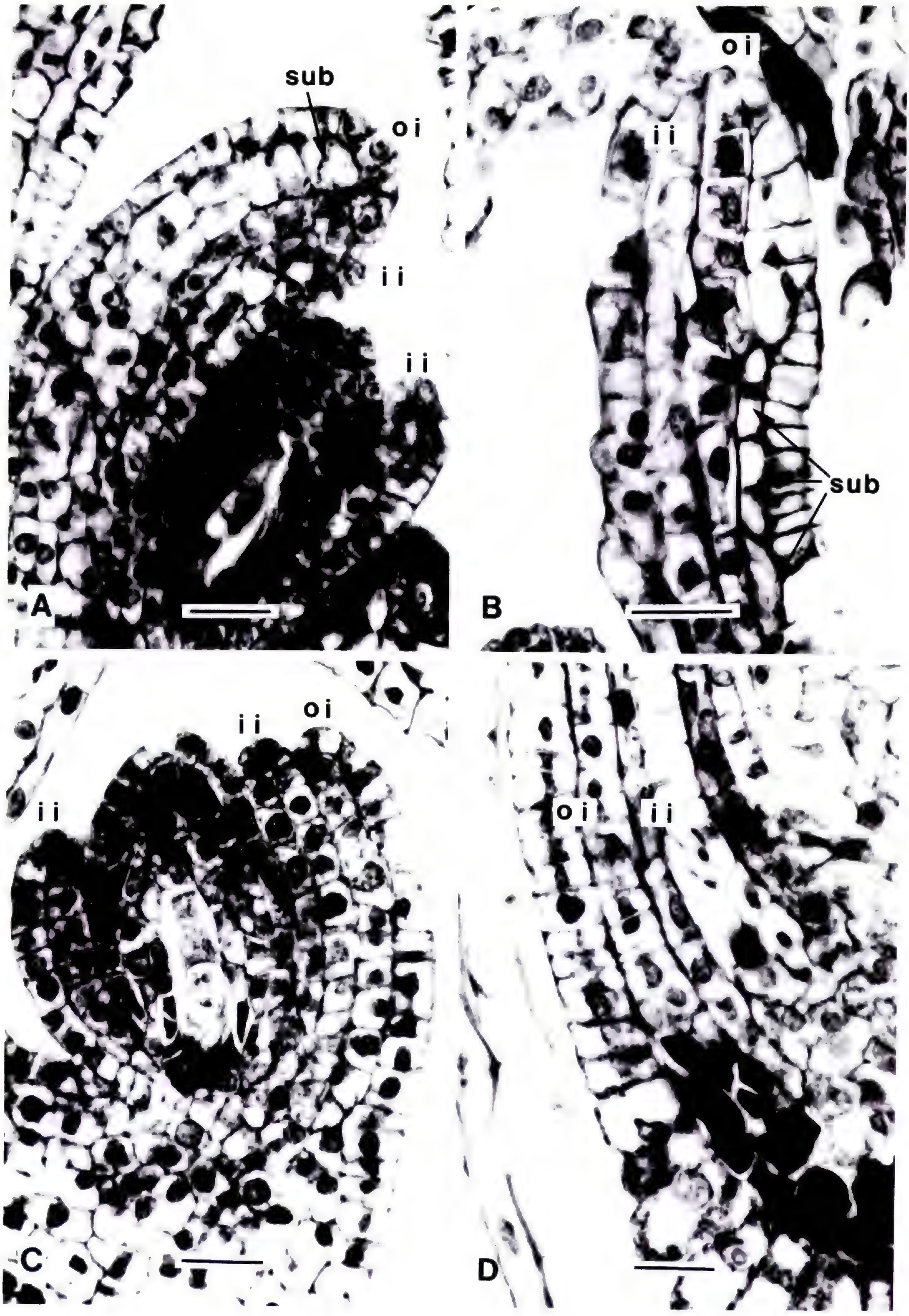


FIGURE 8. *Oenothera flava* subsp. *flava*.—A–C. Median longisections of ovule primordia in progressively successive stages of development, showing that the o.i. is of both dermal and subdermal origin. Note that the derivatives of the dermal initials divide less actively than those of the subdermal ones in the formation of the o.i. Bracket scale = 100 μm.

subdermal origin with the derivatives of the dermal initials dividing less often than those of the subdermal initials subsequently. In some ovules, the derivatives of the subdermal initials extend close to the tip of the o.i. (Fig. 9B).

Clarkia delicata and *C. tenella*—Both the i.i. and the o.i. are of dermal origin and two-layered in both species (Fig. 9C).

Heterogaura heterandra—Both the i.i. and the o.i. are of dermal origin and two-layered.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TRIBE EPILOBIEAE

Boisduvalia glabella and *B. subulata*—Both the i.i. and the o.i. are of dermal origin and two-layered in both species.

Epilobium canum and *E. ciliatum*—Both the i.i. and the o.i. are of dermal origin and two-layered in both species (Fig. 9D).

Discussion

In Table 1 the results of this study on the histogenesis of integuments are presented comparatively. Although all Onagraceae have a two-layered i.i. of dermal origin, four different types of o.i. are recognized with respect to mode of initiation and subsequent growth. These are found in, respectively, 1) *Lopezia* (Lopezieae), *Fuchsia* (Fuchsieae), and *Circaea* (Circaeeae), in which the o.i. is of subdermal origin, and the derivatives of the subdermal initials reach the tip of the o.i. (Fig. 10A); 2) *Oenothera* and *Stenosiphon* (Onagreae), in which the o.i. is of both dermal and subdermal origin, and the derivatives of the subdermal initials extend beyond the middle of the o.i. (Fig. 10B); 3) *Hauya* (Hauyeae) and *Calylophus* and *Gaura* (Onagreae), in which the o.i. is both dermal and subdermal origin, and the derivatives of the subdermal initials are confined to the basal part of the o.i. (Fig. 10C); and 4) *Ludwigia* (Jussiaeeae), *Boisduvalia* and *Epilobium* (Epilobieae), and *Camissonia, Gayophytum, Gongylocarpus,* and *Xylonagra* (Onagreae), in which the o.i. is of dermal origin and mostly two-layered (Fig. 10D).

In angiosperms, the i.i. is almost always of fully dermal derivation and mostly two or three cells thick (Bouman, 1974, 1984); Euphorbiaceae is the only family in which a subdermally initiated i.i. is reported (Bor & Bouman, 1974). Therefore, we could conclude that most Onagraceae have a generalized i.i. with respect to histogenesis and thickness. The amplification in thickness of the i.i. because of periclinal cell divisions, which often is characteristic of *Ludwigia*, would in that case be interpreted as a secondary characteristic (Bouman, pers. comm.).

Bouman (1974, 1984) has postulated that the most primitive type of angiospermous ovule has

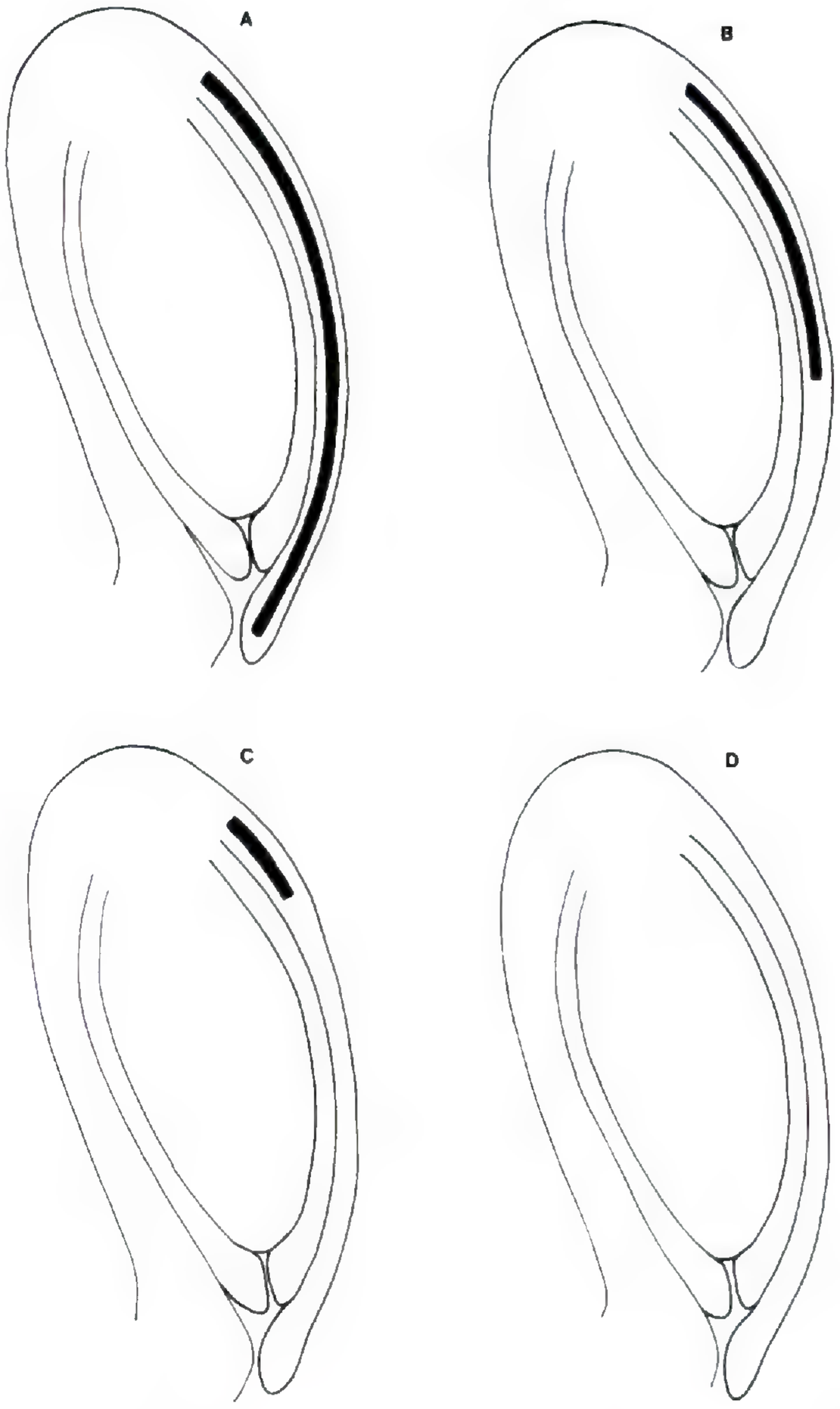

FIGURE 10. Diagrams illustrating four different types of the o.i. with respect to the developmental mode. —A. The o.i. is of subdermal origin.—B. The o.i. is of both dermal and subdermal origin with the derivatives of the subdermal initials dividing more actively than those of the dermal ones.—C. The o.i. of both dermal and subdermal origin with the derivatives of the dermal initials dividing more often than those of the subdermal ones.—D. The o.i. is of dermal origin.

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FIGURE 9. A. *Circaea cordata.* Median longisection of a growing ovule, showing that the o.i. is of subdermal origin and the derivatives of the subdermal initials reach up to the tip of the o.i.—B. *Stenosiphon linifolius.* Longisection of apical part of integuments. Note that, since the o.i. is of both dermal and subdermal origin, a certain part of the o.i. is made up of derivatives of both the dermal and subdermal initials. In this ovule, the derivatives of the subdermal initials extend close to the tip of the o.i.—C. *Clarkia tenella.* Median longisection of a growing ovule showing two-layered i.i. and o.i. of dermal origin.—D. *Epilobium ciliatum.* Longisection of a basal part of a developed ovule showing two-layered i.i. and o.i. of dermal origin. sub, derivatives of the subdermal initials. Scales = 20 μm.

a subdermally initiated o.i. and that thick o.i.'s are more primitive than thinner ones. In light of Bouman's principles, the histogenesis of the o.i.'s of *Lopezia, Fuchsia,* and *Circaea* would be considered the most primitive found in Onagraceae, because in these genera the o.i. is entirely of subdermal origin. At least some species of all three genera have the original basic chromosome number for the family, $n = 11$, and generalized chromosome structure (Kurabayashi et al., 1962; Raven, 1979). As indicated by Eyde and Morgan (1973), *Lopezia, Fuchsia,* and *Circaea* have no evident direct relationship to one another. For example, although both have reduced numbers of flower parts, *Lopezia* differs from *Circaea* in its anther disposition and nectary morphology. *Fuchsia,* despite its mostly red, bird-pollinated flowers and unique fleshy fruits, may be the modern genus closest to the ancestors of most Onagraceae. The pattern of histogenesis of its integuments is in accordance with such a conclusion.

The tribe Onagreae, with ten genera, exhibits three patterns with respect to the histogenetic characters of integuments (see Table 1). Based on Bouman's (1974, 1984) postulates, *Oenothera* and *Stenosiphon* are more primitive than other members of the tribe in that their o.i. retains a stronger tendency to entirely subdermal initiation (see Fig. 10B). *Calylophus* and *Gaura* appear to be more specialized than *Oenothera* and *Stenosiphon,* and less specialized than other Onagreae, in that their o.i. still retains a weak tendency to an entirely subdermal initiation (see Fig. 10C). The remaining six genera, *Camissonia, Gayophytum, Gongylocarpus, Xylonagra, Clarkia,* and *Heterogaura,* in which the o.i. has no tendency to a subdermal initiation (see Fig. 10D), constitute a third group, which on the basis of this feature would be considered the most advanced in the tribe.

It is almost certain that the patterns of integumental histogenesis found in these three groups were derived from one in which the o.i. was entirely of subdermal origin, like that which persists in *Fuchsia, Lopezia,* and *Circaea.* It is not, however, possible to determine whether they were derived sequentially or independently on the basis of this characteristic alone. *Gongylocarpus* is the only genus of Onagreae that retains the original basic chromosome number for the family, $n = 11$, but it has a highly specialized pattern of ovary development (Carlquist & Raven, 1966). If it is an offshoot from the line leading to *Camissonia, Gayophytum,* and *Xylonagra* (Raven, 1964, 1969), then, since all of these genera have identical specialized patterns of integumentary histogenesis in agreement with their distinctive stigma morphology, it would be implied that there is no direct relationship between this line and other Onagreae. Certainly, these relationships make it appear that the reduced basic chromosome number, $n = 7$, must have been derived separately in this line and in the other parts of the tribe.

The large genus *Oenothera* (about 125 species) is identical to the monotypic *Stenosiphon* in the pattern of histogenesis of its integuments, as it is in stigma morphology and other features. Thus the close relationship between these genera first postulated by Raven (1964) is confirmed, but the relationship between these genera and others within the tribe remains obscure. The basic chromosome number, $n = 7$, in these genera certainly seems to have evolved independently from the same number in other genera of Onagreae.

Clarkia and *Heterogaura* share the specialized feature of the o.i. with the first group discussed above. If they are directly related to *Calylophus* and *Gaura,* as claimed by Raven (1964, 1969) on the basis of the thick partitions that divide the sporogenous tissue of their anthers into packets, it would have to be assumed that the pattern of development of their o.i.'s was independently derived from that in the "*Gongylocarpus*—group"; if not, then their specialized anthers and stigmas must have evolved within that group.

Hauya ($x = 10$), now placed in a separate tribe Hauyeae (Raven, 1979) on the basis of the many features, all apparently retained primitive ones, in which it differs from all genera currently assigned to Onagreae, was formerly grouped with *Calylophus, Clarkia, Gaura,* and *Heterogaura* on the basis of its divided sporogenous tissue. The histogenesis of its integuments is identical to that in *Calylophus* and *Gaura,* differing sharply from the more advanced condition found in *Clarkia* and *Heterogaura* and the more primitive one in *Oenothera* and *Stenosiphon.* This may indicate that *Calylophus* and *Gaura* (both $x = 7$) were derived from a phylogenetic line separate from that leading to other Onagreae, and that *Hauya* may be a surviving early evolutionary offshoot of that line. The relationships of the different genera of Onagreae and their affinity to *Hauya* will be discussed in more detail in a separate paper focusing on the exact nature of the divided sporogenous tissue in the Onagraceae (Tobe & Raven, 1985).

The remaining two tribes of the family, Jus-

siaeeae (*Ludwigia* only) and Epilobieae (*Epilobium* and *Boisduvalia*), share with six genera of Onagreae the most advanced type of integumentary histogenesis in the family, with a two-layered o.i. of dermal origin. Fundamental floral differences discussed by Eyde (1977, 1978, 1981) make it clear that *Ludwigia* represents a phylogenetic line different from all other Onagraceae, so that it must have evolved its specialized o.i. independently. There appears to be no evidence to suggest a close grouping of Epilobieae with any genera of Onagreae, so that we may assume that a two-layered o.i. of dermal origin evolved independently in it, in the *Gongylocarpus*-line, and perhaps also in *Clarkia–Heterogaura*—thus three or even four times within Onagraceae. A similar condition has evolved independently in various angiosperms, as for example, Lactoridaceae among "Polycarpicae" (Bouman, 1971).

Within the family, *Ludwigia peploides* (sect. *Oligospermum*) is distinct from all other species in having a three-layered o.i. instead of a two-layered one. Eyde (1977), pointing out that sect. *Oligospermum* stands apart from other ludwigias because of its characteristic aerenchymatous tissue surrounding the endocarp, inferred that this section seems to have diverged early from the other ludwigias and developed its own aquatic adaptations. The characteristic developmental mode of its integuments, unique in Onagraceae, constitutes additional evidence supporting his hypothesis.

This comparative study covering the whole family enables us to evaluate the histogenetic characters of integuments. As has been described and seen in Table 1, this character is nearly genus-specific. Even in cases in which the seed coat or testa histology differs from species to species (e.g., in *Gongylocarpus*, Carlquist & Raven, 1966), the mode of initiation and the subsequent growth of the integuments is consistent within a genus. In view of this, detailed comparisons of this character have made it possible to evaluate the affinities of genera and to consider their relative states of advancement.

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CHROMOSOME NUMBERS IN COMPOSITAE, XV: LIABEAE

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ABSTRACT

Limited but strategic knowledge of chromosome numbers in the small, mostly Andean tribe Liabeae includes records of 12 of the 16 genera: *Cacosmia* ($x = 7$); *Chionopappus* ($n =$ ca. 9); *Ferreyranthus, Oligactis,* and *Liabum* ($x = 18$); *Sinclairia* ($x = 16$); *Paranephelius* ($x = 9, 14$); *Pseudonoseris* ($n =$ 12?); *Erato* ($x = 9$); *Philoglossa* ($n = 18$); *Chrysactinium* ($x = 12$); *Munnozia* ($n = 10, 11, x = 12$). The tribal base number is apparently $x = 9$ supporting a long, separate history from the diploid elements of Vernonieae ($x = 10$) in the Eastern Hemisphere. Apparent aneuploid series of the type seen in *Munnozia* are regarded as reductions from the highest number. No correlation is seen between chromosome number and habit in the tribe. All cytologically known elements of the tribe with extensive distribution beyond the ancestral Ecuadorian–Peruvian area are polyploid. Differences in chromosome number combined with geography provide almost complete generic isolation in the tribe, and no evidence is noted of hybridization between extant genera.

The present paper continues a series dealing with chromosome numbers of Compositae (Raven et al., 1960; Raven & Kyhos, 1961; Ornduff et al., 1963, 1967; Payne et al., 1964; Solbrig et al., 1964, 1969, 1972; Anderson et al., 1974; Powell et al., 1974, 1975; King et al., 1976; Tomb et al., 1978; Robinson et al., 1981) and is the first dealing with the elements of Liabeae as a united group recognized at tribal level. Because data for the tribe are limited, reports from the literature are included in the table with altered identifications where necessary. New reports are provided for 31 populations of 15 species including new reports for nine species and one genus (marked respectively in Table 1).

The new reports in this paper are based on material collected by R. M. King and counted by A. M. Powell and J. F. Weedin. The chromosome counts have been made from aceto-carmine or aceto-orceine squashes of microsporocytes in meiosis. Voucher specimens of the King collections are in US, a second set is in MO.

Robinson (1983a) recognized about 157 species of Liabeae in 15 genera; his paper is the basis for comparison in this paper. The subsequently described monotypic *Bishopanthus* of Peru (Robinson, 1983b) is unknown cytologically and will not be considered in the present study. In spite of the comparatively small size of the tribe, Liabeae show considerable diversity in many structural details (Robinson & Brettell, 1974) and pollen (Skvarla et al., 1977) which are used as the basis for three subtribes, Liabinae, Paranepheliinae, and Munnoziinae, in the recent revision by Robinson (1983a). Present information indicates that the chromosome base numbers in the tribe are also diverse. They correlate to a considerable extent with the revised generic concepts and show distinctive trends in different subtribes.

Previous records of chromosome numbers of Liabeae are scattered and often confusing. Ornduff et al. (1963) offer the only cytological evaluation of Liabeae as a group, but only those parts treated under the traditional concept as subtribe Liabinae in Senecioneae. The traditional disposition, derived from Bentham (1873) and Hoffmann (1894), was totally flawed by the inclusion of foreign elements such as *Neurolaena* and *Schistocarpha,* which are now placed in Heliantheae, by the exclusion of true members of Liabeae such as *Chionopappus, Cacosmia,* and *Philoglossa,* and by the placement of all remaining members of the tribe in a single genus, *Liabum.* Ornduff et al. (1963) were able to mention only one chromosome count of a true member of the tribe, a *Liabum* sp. (*L. ovatum* vel aff.) reported by Diers (1961) as $n = 14$. The chromosome counts available in the unnatural group were said by Ornduff et al. to "attest to the isolated position of the Liabinae."

A number of additional chromosome counts

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TABLE 1. Chromosome numbers and sources for Liabeae.

Species	Chromosome Number (n)	Locality or Literature Source
Cacosmia rugosa H.B.K.	7 (possibly + 1 small fragment)[b]	Ecuador. Azuay: ca. 6 km SE of Cumbe, *King 6702*
	7 (bivalents all same size)[b]	Ecuador. Loja: 7 km W of Loja, *King & Almeda 7889*
Cacosmia rugosa var. *kingii* H. Robinson	7 + 1 small fragment[b]	Ecuador. Loja: ca. 2 km E of Loja, *King 6913*
	7 (bivalents all same size)[b]	Ecuador. Zamora-Chinchipe: 17 km E of Loja, *King & Almeda 7929*
Chionopappus benthamii S. F. Blake	ca. 9 ($2n$ = 18–20)	Peru (Diers, 1961)
Chrysactinium hieracioides (H.B.K.) H. Robinson & Brettell	12	Peru (Turner et al., 1967; as *Liabum*)
	12	Peru (Dillon & Turner, 1982)
	12–14[a]	Ecuador. Loja: 2 km N of Chinchas, *King & Almeda 7962*
	ca. 12 possibly even 13 (or even 14, 15, 16)[a]	Peru. Cajamarca: 41 km NE of Cajamarca, *King & Bishop 9128*
	13 ± 1 (not clear)[a]	Peru. Amazonas: along road SE of Chachapoyas, *King & Bishop 9200*
	12 or 13 [in some cells seemingly clear n = 12; either n = 12 + 1 fragment or 13[II]; 1 very large bivalent (or multivalent?); large bivalent very clear in some cells][a]	Peru. Amazonas: 40 km SW of Leimebamba, *King & Bishop 9245*
	13 ± 1 (in some cells looks like n = 12 or n = 12 + 1 fragment; possibly 12, 13, or 14; heteromorphic bivalents make interpretation difficult; 1 large II and varying sizes down to small, some smaller ones even fragment-looking; bridge seen in few cells so larger "bivalent" possibly is a multivalent)[a]	Peru. Amazonas: 23 km S of Tingo, *King & Bishop 9273*
Chrysactinium rosulatum (Hieron.) H. Robinson & Brettell	12	Peru (Dillon & Turner, 1982; as *C. acaule*)
	13 or 14 [1 larger bivalent, 3 moderate-sized bivalents, other smaller bivalents (seemingly); heteromorphic bivalents make it difficult to interpret (possibly even n = 12[II])][a]	Peru. Cajamarca: 55 km NE of Cajamarca, *King & Bishop 9139*

TABLE 1. Continued.

Species	Chromosome Number (*n*)	Locality or Literature Source
Erato polymnioides DC.	9	Ecuador (Olsen, 1980; as *Munnozia*)
Erato vulcanica (Klatt) H. Robinson	9	Colombia. Putumayo (Jansen et al., 1984; as *Liabum*)
	9	Colombia (Olsen, 1980; as *Munnozia*)
	9	Colombia (Turner et al., 1979; as *Liabum* cf.)
Ferreyranthus rugosus (Ferreyra) H. Robinson & Brettell	ca. 18	Peru (Turner et al., 1967; as *Liabum*)
Ferreyranthus verbascifolius (H.B.K.) H. Robinson & Brettell	19 ± 1 (heteromorphic bivalents)[a]	Ecuador. Azuay: ca. 9 km N of Sigsig, *King 6647*
Liabum bourgeaui Hieron.	report of 9 believed in error (see text)	(Olsen, 1980)
Liabum eggersii Hieron.	ca. 20 + 1, 2 fragments[a]	Ecuador. Guayas: ca. 12 km SE of Vinces, *King 7010*
Liabum floribundum Less.	18	Peru (Dillon & Turner, 1982)
	19 + 2[a]	Ecuador. Tungurahua: 7 km E of Baños, *King 6541*
	ca. 20[a]	Ecuador. Azuay: ca. 14 km SW of Girón, *King 6686*
	19[a]	Ecuador. Azuay: ca. 5–6 km NE of Cuenca, *King 6875*
	19 + 6, 7 fragments[a]	Ecuador. Chimborazo: ca. 39 km NE of Bucay, *King 6961*
	ca. 19 [seemingly 19^{II} and 3 round fragments or I's; appear to be 17 major bivalents; these heteromorphic, with 2 of these smaller than all the others (interpreted as II's if $n = 19^{II}$) and precociously separating by metaphasis I][a]	Ecuador. Cañar: 67 km E of Cañar, *King & Almeda 7795*
Liabum kingii H. Robinson	17–20[a]	Ecuador. Tungurahua: ca. 2 km E of Río Negro, *King 6555*
Liabum melastomoides (H.B.K.) Less.	19[a]	Colombia. Valle del Cauca: Cordillera Central, vertiente occidental, piedemonte entre La Uribe y Astelia (Bugalagrande-Sevilla), Vuelta de Violin, *Cuatrecasas & Cuadros 28932*
Liabum subacaule Rydb.	18	Dominican Republic (Torres & Liogier, 1970)
Munnozia ferreyrii H. Robinson	12	Peru (Dillon & Turner, 1982)
Munnozia hastifolia (P. & E.) H. Robinson & Brettell	11 (with 1 large pair)[a]	Ecuador. Tungurahua: ca. 2 km E of Río Negro, *King 6562*
	12[a]	Ecuador. Pastaza: ca. 18 km N of Puyo, *King 6569*
Munnozia jussieui (Cass.) H. Robinson & Brettell	ca. 13	Ecuador (Jansen & Stuessy, 1980; as *Liabum*)
	12	Colombia. Nariño (Jansen et al., 1984; as *Liabum*)
Munnozia lyrata (A. Gray) H. Robinson & Brettell	ca. 24	Peru (Dillon & Turner, 1982)

TABLE 1. Continued.

Species	Chromosome Number (*n*)	Locality or Literature Source
Munnozia maronii (Andre) H. Robinson	12 + 1[a]	Bolivia. Cochabamba: 25 km from Colomi on road to Tunari, *King & Bishop 7687*
Munnozia senecionidis Benth.	10	Colombia (Powell & King, 1969; as *Liabum megacephalum*)
	10	Colombia. Cundinamarca (Jansen et al., 1984; as *Liabum sagittatum*)
	ca. 12[a]	Ecuador. Loja: ca. 8 km E of Loja, *King 6918*
	10 (8 normal-sized bivalents and 2 bivalents twice the normal size; the large bivalents possibly multivalents but behaving like bivalents)[a]	Ecuador. Azuay: 8–10 km S of Cumbe, *King & Almeda 7773*
	10 ? (same as *7773*, except noted that some of 8 smaller bivalents slightly heteromorphic. See text)[a]	Ecuador. Loja: 10 km S of Seraguro, *King & Almeda 7834*
	10 (same as *7834*)[a]	Ecuador. Loja: 2 km E of Loja, *King & Almeda 7909*
Oligactis pichinchensis (Hieron.) H. Robinson & Brettell	ca. 39	Ecuador (Jansen & Stuessy, 1980; as *Liabum*)
	ca. 18	Colombia. Cundinamarca (Jansen et al., 1984; as *Liabum*)
Paranephelius jelskii (Hieron.) H. Robinson & Brettell	9	Peru (Turner et al., 1967; as *Liabum bullatum*)
Paranephelius ovatus Wedd.	14, 15[a]	Bolivia. Cochabamba: at Cholla, *King & Bishop 7540*
Paranephelius uniflorus P. & E.	14	Peru (Diers, 1961; as *Liabum ovatum* vel aff.)
Philoglossa peruviana DC.?	18	Peru (Diers, 1961; as *Philoglossa pterocarpha*)
Pseudonoseris szyszylowiczii (Hieron.) H. Robinson & Brettell	12 (questioned in text)	Peru (Dillon & Turner, 1982)
Sinclairia discolor Hook. & Arn.	17, 18	Mexico (Powell et al., 1974; as *Liabum*)
Sinclairia hypochlora (S. F. Blake) Rydb.	15 or 16 (*n* = 15 with one large bivalent or *n* = 16; bivalents heteromorphic and abnormal)[a]	Guatemala. Suchtepequez: ca. 30 km W of Mazatenango, *King 7245*
Sinclairia sublobata (B. L. Robinson) Rydb.	15, 16 (*n* = 15 with one bivalent extra large, or *n* = 16, or possibly even *n* = 17)[a]	Guatemala. Escuintla: ca. 22 km SW of Amatillán, *King 7171*
	16 (multinucleolate, 1 large, 1–3 smaller; appears to be *n* = 15, 16 pairs at diakinesis not forming characteristic shapes; bivalents different size)[a]	Guatemala. Quezaltenango: ca. 18 km S of Quezaltenango, *King 7258*

[a] New reports.
[b] First report for genus.

have become available for the group since the earlier summary, some as a result of recognition of the previously reported *Philoglossa* and *Chionopappus* (Diers, 1961) as members of the tribe, others as a result of new reports. Nordenstam (1977), in his short summary of the tribe, cited chromosome numbers for seven genera. Dillon and Turner (1982) gave reports for four genera.

The few reports in recent years by other authors, and the reports in the present study are still limited in number, but the total is now sufficient to see some patterns in the tribe that have not been evident before. The rather complete understanding of the tribe on the basis of other characters (Robinson, 1983a; Robinson & Marticorena, unpubl. data) has aided further and provides a basis for important phyletic conclusions.

The reports in the present paper represent a small return on many attempts. The members of the Liabeae are much less easily counted than most members of such tribes as the Eupatorieae (King et al., 1976) or Heliantheae (Robinson et al., 1981). However, the various ways in which chromosomes are difficult to count are themselves characters worthy of study, and are often characteristic of genera or tribes. One example in the subfamily Asteroideae (sensu Robinson, 1977) is *Mikania* in the normally rather easily counted Eupatorieae. *Mikania* seems to have some variation in the actual number of chromosomes, but the primary difficulty lies in the slight differential in the stainability of the chromosomes and the cytoplasm. The chromosomes stain poorly and the cytoplasm takes enough stain to make the chromosomes difficult to count. Most of the examples of less easily counted Asteraceae, however, are in Cichorioideae (sensu Robinson, 1977) in which Liabeae is included. Collections of Mutisieae, Vernonieae, and Liabeae all seem to yield characteristically poor results.

The comparison of this feature that is particularly important is that between Liabeae and Vernonieae, because the former have often been included in the latter in spite of their opposite leaves, rays, yellow corollas, and frequent milky sap (Cassini, 1823, 1825, 1830; Nash, 1976; Jansen & Stuessy, 1980). That both tribes have chromosomes that are difficult to count might be taken as an indication of relationship, but according to the observations by Powell, the nature of the problem in the two tribes is not the same. In Liabeae there are uncertainties in the interpretation of heteromorphic bivalents that appear to occur in many of the genera (e.g., *Chrysactinium, Liabum, Munnozia*). When the heteromorphic meiosis I configurations occur, one or two of them appear to be much larger bivalents (or multivalents?), and then the other bivalents occur in varying sizes down to small, with some of the smaller configurations often resembling fragments in size and shape. When bud material is adequate it is often possible to resolve uncertain counts by observing meiotic chromosome behavior through several stages. In Liabeae, however, aceto-carmine staining is often poor at prophase I stages before and through diakinesis. Metaphase I and anaphase I chromosomes usually stain deeply with aceto-carmine. In Vernonieae, aceto-carmine preparations often reveal poorly stained bivalents that remain clumped or "sticky" in meiosis I stages. According to Sterling Keeley (pers. comm.), Vernonieae yield better results when collected at midday, a trait not tested for in Liabeae.

Cytological Evidence Regarding Original Chromosome Number and Relationships

In many tribes in the Asteraceae, original base numbers have been determined with reasonable confidence (Senecioneae—Ornduff et al., 1963; Eupatorieae—King et al., 1976; Heliantheae—Robinson et al., 1981). The various chromosome numbers known for Liabeae are adequate for a similar determination for that tribe.

There have been various proposals of a base number for the Asteraceae, but only two are regarded here as credible. The number $x = 9$ with its multiples is most common in the family (Solbrig, 1977) and has been suggested as the base number for the family by Raven (1975). More recently, Robinson et al. (1981) have suggested $x = 10$ as a base number for at least the entire subfamily Asteroideae. Evidence of predominant decreasing aneuploidy in Asteraceae would favor $x = 10$ as ancestral in most Cichorioideae as well. Still, internal evidence from Liabeae does not fully agree with the external evidence. The most common chromosome numbers in the tribe seem to be $n = 9$ and $n = 18$ or ca. 18. The counts of $n = 9$ seem centrally located in the tribe and have been cited from elements of all three subtribes. The number $n = 10$ is reported, perhaps

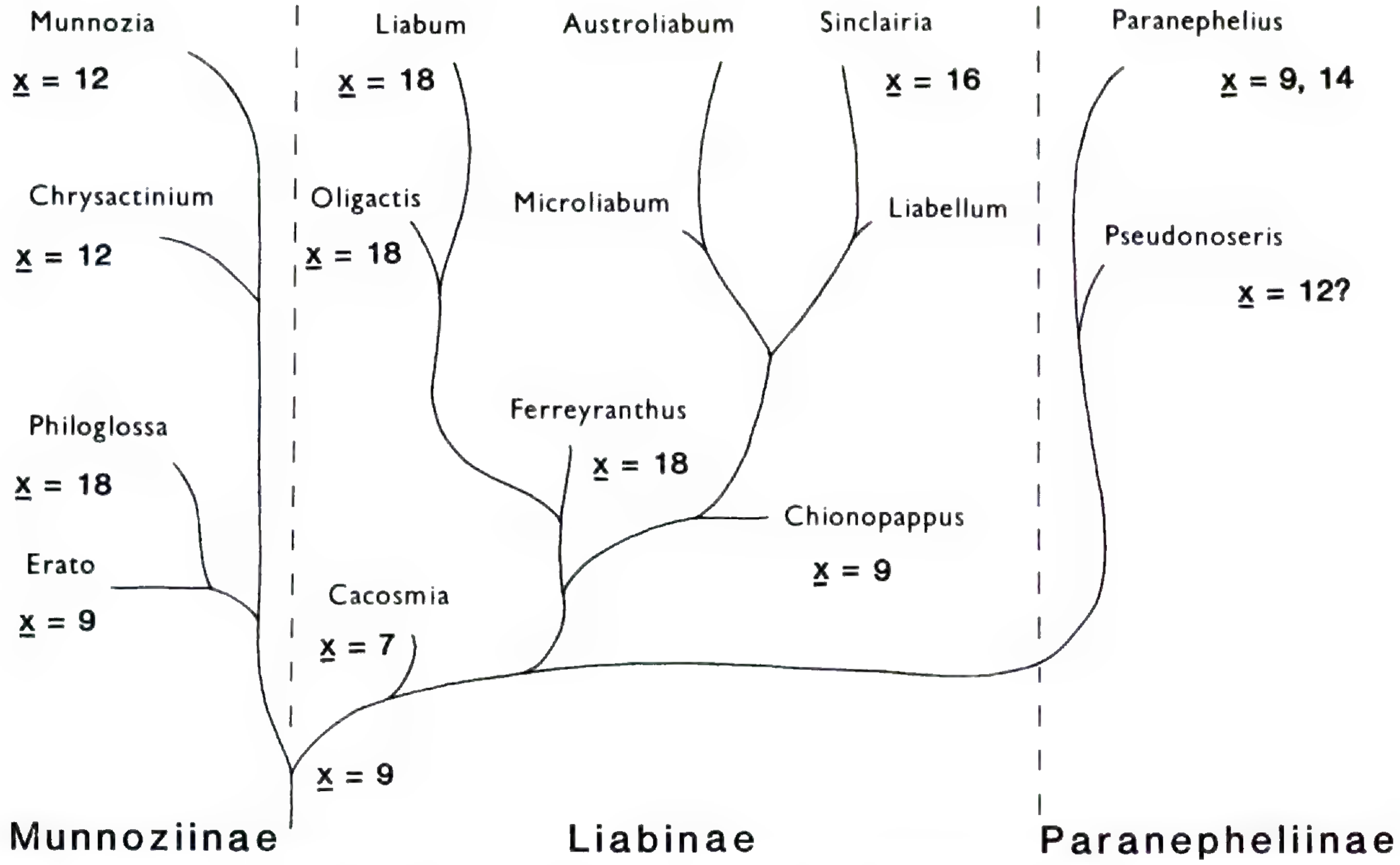


FIGURE 1. Schematic representation of possible relationships of genera and subtribes of the Liabeae (from Robinson, 1983a) with postulated basic chromosome numbers inserted.

erroneously, in *Munnozia* but in a comparatively specialized element of that genus (Robinson, 1983a) as explained below. A base of $x = 9$ would explain adequately all the elements of the Liabeae, and there is no need to assume a higher base of $x = 10$ within the reconstructible history of the tribe. No evidence of an ancestral $x = 10$ survives in extant Liabeae.

The basic chromosome number in Liabeae and the pattern of variation in chromosome numbers both furnish significant contrasts from other elements of the family which have been considered related. The base of $x = 9$ and the lack of stability in the chromosome number in the tribe contrast with the nearly consistent $n = 10$ of Senecioneae in which members of the Liabeae were traditionally placed (Bentham, 1873; Hoffmann, 1894). This provides some additional support for the removal of Liabeae from the Asterioidean Senecioneae, which has been proposed by numerous recent workers (Robinson & Brettell, 1974; Wagenitz, 1976; Nordenstam, 1977; Nash, 1976; Jansen & Stuessy, 1980; Robinson, 1983a).

Most of these recent workers place Liabeae near or in Vernonieae in the series of tribes presently included in the expanded Cichorioideae (or a segregate group Vernonioideae Turner ex Jansen & Stuessy, 1980). It is Vernonieae to which Liabeae have closest resemblance in the general aspect of their styles, anthers, and pappus. The base number of either $x = 9$ or 10 suggested by Jones (1977) for Vernonieae, refined to a probable $x = 10$ by Robinson et al. (1981), is not significantly different from that in Liabeae. Nevertheless, actual relationships between the two tribes may not be as direct as many authors suppose, since there are significant differences in morphological, anatomical, and palynological characters. A more careful analysis of the cytology reveals an important discrepancy between the tribes in chromosomes as well. In the Vernonieae, the $x = 10$ is characteristic of the Paleotropical elements and various specialized elements that evidently recently dispersed from that area (Jones, 1977). In contrast, the Neotropical elements, that overlap geographically with Liabeae, have chromosome numbers of $x = 19$ (Funk in Turner, 1981) and $x = 17$ derived from polyploids of $x = 10$. On the basis of present evidence, $n = 10$ is not represented in the basically American elements of the Vernonieae. This raises the possibility that the Vernonieae were originally restricted to the Paleotropical Region and were initially introduced into the Western Hemisphere in a polyploid condition.

Liabeae are strictly Andean in origin, with a

series of chromosome numbers that seem to be based on an original $x = 9$. These numerical and geographical discrepancies, correlated with morphological, anatomical, and palynological discrepancies (Robinson, 1983a; Robinson & Marticorena, unpubl. data), suggest that the two tribes had separate origins in separate hemispheres and that their common ancestor is quite remote.

Review of the Chromosome Numbers

The following discussion of chromosome numbers in Liabeae follows the three subtribal groupings of Robinson (1983a). For purposes of orientation, it should be noted that according to Robinson, Liabinae and Munnoziinae appear to represent a basal divergence in the tribe, and Paranepheliinae seem to have arisen from slightly more advanced members of Liabinae. As such, all three subtribes contain elements showing comparatively primitive characters.

LIABINAE

As shown below and in Table 1, and as summarized in Figure 1, genera of the subtribe fall into two groups. The first has chromosome numbers apparently consistently at $n = 7$ or 9, and the second has numbers apparently consistently near $n = 16$ or 18. The latter group includes all of the more widely distributed and more richly speciated genera of the subtribe.

A series of new reports clearly establishes $x = 7$ as the chromosome number for *Cacosmia,* and it is the only known occurrence of the number in the tribe. It is not difficult to interpret $x = 7$ as a reduction from $x = 9$ that seems basic in the tribe, although *Cacosmia* is a shrub, and such reduction usually involves reduction in the habit to less woody or shorter-lived plants (Bennett, 1972; Robinson et al., 1981). The primary traditional distinction of *Cacosmia,* the lack of the pappus, along with such features as the ranked involucral bracts and the modified arrangement of thickenings in the endothecial cells (Robinson, 1983a) do not justify placement in a separate tribe such as the Helenieae (Bentham, 1873) but do indicate some phyletic distance. The genus can be interpreted as one of the earliest divergences from the basal stock of the subtribe with a unique cytological history. Overwhelming evidence from other tribes and from other Liabeae against a base of $x = 7$ and against frequent aneuploid increase (Robinson et al., 1981) prohibits the acceptance of $x = 7$ as the forerunner of $x = 9$ in Liabeae. Furthermore, some specialized aspects of *Cacosmia* discourage any thought of a direct connection between the $x = 7$ of *Cacosmia* and the $x = 12$–14 of various Munnoziinae and Paranepheliinae.

Chionopappus of coastal Peru has been reported to have $n =$ ca. 9 by Diers (1961), and this is the only report of the supposed tribal base number in Liabinae. The genus is distinguished by its uniseriate plumose pappus and was originally placed in Mutisieae (Bentham, 1873). Other features of *Chionopappus,* however, are not unusual for Liabinae. The $n = 9$ in the genus indicates a point of origin in the subtribe before the incidence of polyploidy that characterizes the advanced genera, a point similar to the ones at which *Cacosmia* and the Paranepheliinae may have diverged.

The remaining known chromosome numbers in Liabinae are apparently at the polyploid level. In *Ferreyranthus* of Peru and southern Ecuador, there are reports of $n = 18$ or 19 plus or minus 1 on the basis of two closely related species. In this genus, polyploidy is associated with the most subarborescent members of the tribe, but the habit difference from genera such as *Cacosmia* is not sufficiently marked to indicate any particular correlation with polyploidy. There is no reason to assume that polyploidy in *Ferreyranthus* is anything but a part of the general polyploid trend in the more advanced members of Liabinae.

The majority of the chromosome reports from the subtribe are from *Liabum* and *Oligactis.* The two genera are centered geographically in the Andes of Colombia and Ecuador, but *Liabum* has attained the widest range of any genus in the tribe, from central Mexico and the Greater Antilles to Bolivia. The various reports indicate a chromosome number of $n = 18$ or 19. Because of the difficulties in counting chromosomes in the tribe, it is uncertain whether the variety in reports represents a true variety in numbers. The presence of a probable base of $x = 9$ in the tribe causes the present authors to favor $x = 18$ as basic for *Liabum, Oligactis,* and *Ferreyranthus.* The $n =$ ca. 39 reported from *Oligactis pichinchensis* indicates a further level of polyploidy in the group.

The report of $n = 9$ for *Liabum bourgeaui* by Olsen (1980) is anomalous in view of all other evidence for the generic group. Also, the species occurs in Mexico and Central America, but not in Colombia from where the collection is cited. The voucher from SWMT is actually *Verbesina*

barragana Cuatrecasas or a closely related species, which casts total doubt on the report because $n = 9$ is not characteristic of either genus. Unfortunately there are no other reports for *L. bourgeaui* or of its two closest relatives, *L. asclepiadeum* Schultz-Bipontinus of the northern Andes or *L. ferreyrii* H. Robinson of Peru.

The *Sinclairia* group of Mexico and Central America has been reported as $n = 17, 18$ by Powell et al. (1974) and Nordenstam (1977) on the basis of a single count of *S. discolor*. It seems notable that this report was uncertain toward a lower number from $n = 18$ because the present study shows $n = 15, 16$ for the genus on the basis of a number of species with one apparently clear count of $n = 16$. In the absence of better evidence, the $x = 16$ is regarded here as basic for the group.

Sinclairia, Ferreyranthus, and the genus-pair *Liabum* and *Oligactis* all have higher numbers of chromosomes presumably derived from polyploidy, but these comparatively advanced members of the subtribe may not share the same polyploid ancestry. Certainly, *Sinclairia* has structural features and latex that suggest closer relationship to *Chionopappus* with $n =$ ca. 9 than to the other polyploid genera.

PARANEPHELIINAE

The subtribe contains *Paranephelius* and *Pseudonoseris*. As can be seen in the table, there are only three chromosome number reports for *Paranephelius* showing two basically different numbers. The new report of $n = 14$ or 15 for *Paranephelius ovatus* supports the report of $n = 14$ ($2n = 28$) by Diers (1961: 465), although Diers's report for *P. ovatus* vel aff. from coastal Peru probably represents the closely related *P. uniflorus* Poepp. & Endl. At the same time, the $n = 9$ reported by Turner et al. (1967) for *P. jelskii* (as *P. bullatus*) fits well into the concept of $x = 9$ as a base for the tribe and is reported from the most divergent element in the genus. The element for which this ancestral number is reported is restricted in distribution in Amazonas in northern Peru while the probable derived group with $n = 14$ is widely distributed from more coastal northern Peru south to Bolivia and northernmost Argentina. These counts do not provide a basis for much speculation on the actual origin of the $n = 14$, but some numbers in the $n = 11$, 12 range occur in the *Munnozia* element of the Munnoziinae where possible patterns in the origin of such aneuploid increases are discussed more fully.

The recent report of $n = 12$ from *Pseudonoseris szyszylowiczii* (Dillon & Turner, 1982) seems somewhat anomalous and needs confirmation. As reported, the number would represent an additional aneuploid increase in the subtribe separate from that cited above within *Paranephelius*. We hesitate to accept the present report because the voucher from F, collected 5 Jan. 1979, and a duplicate at US, while correctly determined, show only mature heads, a condition, which according to R. M. King is typical of the species at that time of year. It seems possible that the buds counted might have come by error from some intermixed *Munnozia* or *Chrysactinium* in which the number $n = 12$ is common.

MUNNOZIINAE

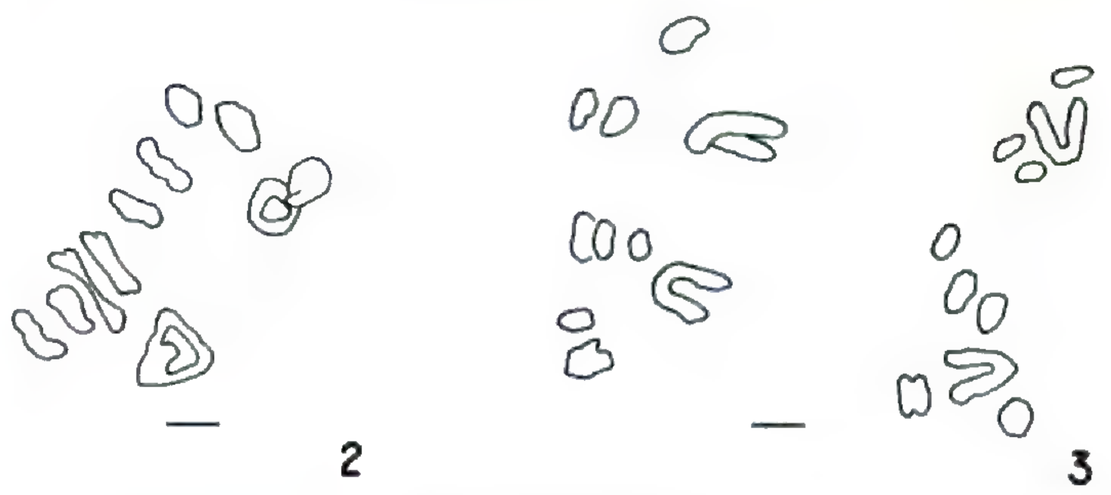
The subtribe contains four genera that fall easily into two groups, *Erato–Philoglossa* and *Chrysactinium–Munnozia,* on the basis of pubescence, endothecial cell structure, and pollen structure (Robinson, 1983a; Robinson & Marticorena, unpubl. data). Chromosome reports in Table 1 and the summary in Figure 1 show that the two groups are distinct cytologically also.

Erato and *Philoglossa* have ranges that broadly overlap in the central Andes south to Bolivia, but *Erato* is concentrated in the main Andean chains that reach north to Venezuela and Colombia with an extension to Costa Rica, whereas four of the five species of *Philoglossa* are restricted to the coastal ranges of Peru. The two genera have been placed in separate tribes in the traditional systems of classification of Bentham (1873) and Hoffmann (1894), although they prove intimately related on the basis of all characters except their pappus. The two genera share most notably a stiff type of vegetative hair, short, transversely polarized endothecial cells, a reduced number of ribs on the achene, a somewhat irregularly spinulose pollen, and a chromosome number based on $x = 9$. *Philoglossa* is generally more advanced in its more reduced pappus and its two rather than four ribs on the achene. Reports by Turner et al. (1979), Olsen (1980), and Jansen et al. (1984) firmly establish $n = 9$ as the number for *E. vulcanica*. Unfortunately, a number of attempts to count the closely related *E. polymnioides* DC. during the present study have failed, but one count of $n = 9$ has been provided by Olsen (1980). The report of $n = 18$ for *Phil-*

oglossa stenocarpa by Diers (1961) fits well with the $n = 9$ reported from the closely related *Erato*. The limited examples give little indication of the full distribution of polyploidy in the two genera; nevertheless, the polyploidy in the smaller though not necessarily more herbaceous *Philoglossa* is still another example of the lack of correlation between habit and chromosome number in the tribe.

Chrysactinium and *Munnozia* also have geographic ranges that overlap in the Andes of Ecuador and northern Peru, but the latter, larger genus extends much more widely to Costa Rica, Venezuela, and Bolivia. The two genera share a tomentose type of vegetative pubescence, vertically or obliquely polarized endothecial cells, usually ten-ribbed achenes, pollen with regularly distributed spinules, and chromosome numbers of $n = 10$ to ca. 13. *Chrysactinium hieracioides* now has many reports by Turner et al. (1967), Dillon and Turner (1982), and the new reports (see Table 1) indicate a chromosome number of $n = 12$, the same number reported from the Peruvian species *C. rosulatum* (as *C. acaule*, Dillon & Turner, 1982). The new report of $n = 13, 14$ in *C. rosulatum* (see Table 1) and reports of possible $n = 13$ in *C. hieracioides* may or may not represent true variation in the genus, but the reports of $n = 12$ seem more reliable, and that number also seems basic in the closely related *Munnozia*. In the examination of the King collections of *Chrysactinium* from Peru (*9128, 9139, 9200, 9245, 9273*), Powell noted a uniformity of karyotype that contrasted with that of a *Ferreyranthus* studied with uncertain results at the same time.

In *Munnozia*, most reports are based on *M. senecionidis* and indicate a chromosome number of $n = 10$ or 11. There is one report of $n =$ ca. 12 (see Table 1). However, on the basis of the drawings provided (Figs. 2, 3), Strother (pers. comm.) suggests the report of $n = 10$ is in error. He suggests that the cell illustrated in Figure 2 exhibited $8_{II} + 2_{IV}$ for $2n = 24$ or $10_{II} + 1_{IV}$ for $2n = 24$. This presumes that the larger configurations noted by Powell are actually multivalents even though they exhibited meiotic behavior that is characteristic of bivalents. Other species representing the great diversity of the genus, including *M. jussieui* (Jansen & Stuessy, 1980), *M. lyrata* and *M. ferreyrii* (Dillon & Turner, 1982), and *M. hastifolia* and *M. maronii* reported here, show mostly $n = 12$ or ca. 13 or $n =$ ca. 24, which



FIGURES 2, 3. *Munnozia senecionidis* Benth. *King and Almeda 7834*.—2. Metaphase I.—3. Anaphase II. Line = 4 μm.

agrees more with *Chrysactinium*. On this basis we regard $x = 12$ as basic for the generic pair.

The $x = 12$ of the *Chrysactinium–Munnozia* group and the $x = 14$ of typical *Paranephelius* appear to be two clear examples of aneuploid gain in Liabeae in spite of the evidence from other groups such as Heliantheae (Robinson et al., 1981) regarding the comparative rarity of such gains in chromosome number. We have no inclination to regard either number as the result of polyploidy from numbers lower than $n = 9$, and neither group shows any evidence of close relationship to the one genus in the tribe, *Cacosmia*, having a chromosome number less than $n = 9$. As already indicated, there is also no close relationship between the *Munnozia* group and *Paranephelius*, and the two examples of aneuploid gain are thus totally independent. There is, however, no need to accept more than one instance of aneuploid gain in *Munnozia*. The series of numbers in *Munnozia* is at best a downward series that occurs in a specialized element of the genus. The $n = 12$ is basic to both genera and is obviously ancestral in the group. The occasional reports of still higher numbers in the *Munnozia* group might indicate that the ancestral number of the generic pair was actually higher than $n = 12$. Although no direct evidence is available, the apparent increasing aneuploidy might derive from some extinct polyploid ancestor having $n = 18$.

It is notable that series of numbers above the ancestral base number similar to those in *Munnozia* can be found in other tribes of Asteraceae. One such example is in the *Microspermum–Stevia–Piqueria* relationship of Eupatorieae. At present we favor an interpretation of that series like that of *Munnozia* with the highest number in the series being the first, followed by reduction. We suspect that many other seeming series of aneuploid increases should be interpreted in this way.

GENERAL CONCLUSIONS

Given the overall pattern of chromosome numbers in the Liabeae, there remain two general points of interest to be discussed.

The foregoing discussion of the genera and subtribes includes mention of many examples of polyploidy in the tribe, mostly concentrated in two series of advanced members of Liabinae. There seems to be an unusual lack of correlation of chromosome number with habit in the tribe, with little tendency for lower numbers in shorter-lived or more herbaceous plants as commonly occurs in other tribes (King et al., 1976; Solbrig, 1977) and in many other groups of plants. However, the polyploids in Liabeae do include all the elements that have their primary ranges north of the Ecuadorian–Peruvian center of the tribe. It is as though the diploid members of the tribe were restricted to their ancestral area, and only polyploids were able to invade new territories. This provides the possibility of an interesting test. Among the genera not yet counted is *Austroliabum*, a genus that has exceeded the ancestral range of the tribe to the south in Bolivia and Argentina. If the hypothesis is correct, then this genus should also be polyploid.

It has been observed (Robinson, 1983a) that intergeneric hybridization has left its mark on many of the large tribes of Asteraceae and may be an important factor in their success. However, there is no evidence of such hybridization in the Liabeae, and it has been suggested that this is correlated with the comparatively restricted size and distribution of the tribe. The present genera of Liabeae that are not geographically isolated tend to have different chromosome numbers, which would inhibit hybridization. The number of different basic numbers represented is remarkable considering the small number of extant genera (Fig. 1). From a cytologically uniform group of ancestors, *Cacosmia* can be seen as an early drop-out with reduction of its chromosome number to $n = 7$, whereas other genera became isolated by various higher chromosome numbers or by geography.

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CHROMOSOME STUDIES ON *HYDROMYSTRIA LAEVIGATA* (HYDROCHARITACEAE)[1]

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ABSTRACT

Chromosomes of individuals from two Argentine populations of *Hydromystria laevigata* (Willd.) A. T. Hunz. were analyzed for numbers, meiotic behavior, and karyotype. It has $n = 14$ and $2n = 28$. Both populations have regular meiosis and show no significant statistical differences between them. The karyotype is similar in both populations: asymmetrical and bimodal; it is formed by: 4 *m* pairs + 6 *sm* pairs + 4 *st* pairs. No satellites were found.

Hydromystria is a monotypic genus of Hydrocharitaceae. The only species, *H. laevigata,* is an aquatic plant that grows in Mexico, West Indies, and South America (Hunziker, 1981, 1982). Some authors include *Hydromystria* within *Limnobium* (Dandy, 1959; Cook et al., 1974; Cook & Urmi-König, 1983), while others recognize them as distinct monotypic genera although closely related (cf. Hunziker, 1981, 1982).

No comprehensive cytological study has been carried out on *H. laevigata,* although some chromosome counts have been published. Geitler (1938; sub *Trianea bogotensis* Karst.) reported $2n = 26$–28, and the same author (1940) found $4n = 56$ in counts on colchicine-induced tetraploid root cells. Recently, Urmi-König (in Cook & Urmi-König, 1983) reported five different chromosome numbers for this plant [sub *Limnobium laevigatum* (Willd.) Heine]: $2n = 26, 27, 28, 29, 30$. In the present contribution, the somatic and gametic numbers of two Argentine populations of *H. laevigata* are reported, as well as their meiotic behavior and karyotype.

MATERIALS AND METHODS

The materials came from two morphologically identical populations (hereafter named P_1 and P_2) collected in the following localities: Argentina, Córdoba: P_1 = Punilla: Cabalango, *Bernardello, Weigel & Moscone 359 bis,* 29 Aug. 1982; P_2 = Calamuchita: Emblase Río III, camino a la segunda Usina, *Moscone, Carrizo & Moscone 1,* 24 Oct. 1982; we analyzed 35 plants of P_1 and 16 of P_2. Voucher specimens have been deposited in the herbarium of Museo Botánico de Córdoba, Argentina (CORD).

Mitotic chromosomes were examined in root tip squashes; the root tips were fixed in 1 : 3 acetic acid : ethanol mixture after pretreatment in a saturated solution of p-dichlorobenzene in water for 5–7 hours at room temperature, and then stained with alcoholic hydrochloric acid carmine (Snow, 1963) for at least 12 hours. Karyograms were prepared from microphotographs, using the terminology introduced by Levan et al. (1964). Two parameters were used: the arm ratio and the centromeric index. The chromosomes were first arranged according to their increasing arm ratio and then according to the decreasing order within each group. The idiogram is based on ten metaphase plates (five from each population).

Meiotic behavior was observed in pollen mother cells obtained by squashing young anthers fixed in 1 : 3 acetic acid : ethanol and stained with acetic carmine. All the permanent mounts were made with Bradley's method (1948). The statistical methods followed Sokal and Rohlf (1979); as regards the *t*-test, the levels of significance considered were 0.05 and 0.01.

RESULTS

Meiotic observations. Table 1 summarizes the data obtained from the analysis of meiotic behavior. Both populations have regular meiosis, forming usually 14 bivalents (Fig. 1A, B). Sometimes univalents were observed: a 13 II + 2 I configuration was detected in 2.2% of P_1 cells and in up to 3.3% of P_2 cells.

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TABLE 1. Meiotic behavior of *Hydromystria laevigata.*

Population	Chromosome Number (n)	Chromosomal Associations in Diplotene-Diakinesis per Cell: Range and Mean ± Standard Error					Mean of Chiasmata per Chromosome Pair: Mean ± Standard Error	Number of Studied Cells
		II	I	Ring II	Chiasmata Total	Terminal Chiasmata		
P_1	14	13–14 13.98 ±0.022	0–2 0.044 ±0.044	1–9 4.73 ±0.295	16–25 20.78 ±0.365	10–19 15.58 ±0.319	1.48 ±0.026	45
P_2	14	13–14 13.97 ±0.019	0–2 0.065 ±0.037	1–8 4.53 ±0.168	15–25 20.83 ±0.226	7–20 15.15 ±0.260	1.49 ±0.016	92
t-test		$t_{135} = 0.32$ $P \cong 0.7$	$t_{135} = 0.34$ $P \cong 0.7$	$t_{135} = 0.63$ $P \cong 0.5$	$t_{135} = 0.12$ $P \cong 0.9$	$t_{135} = 0.99$ $P \cong 0.3$	$t_{135} = 0.34$ $P \cong 0.7$	

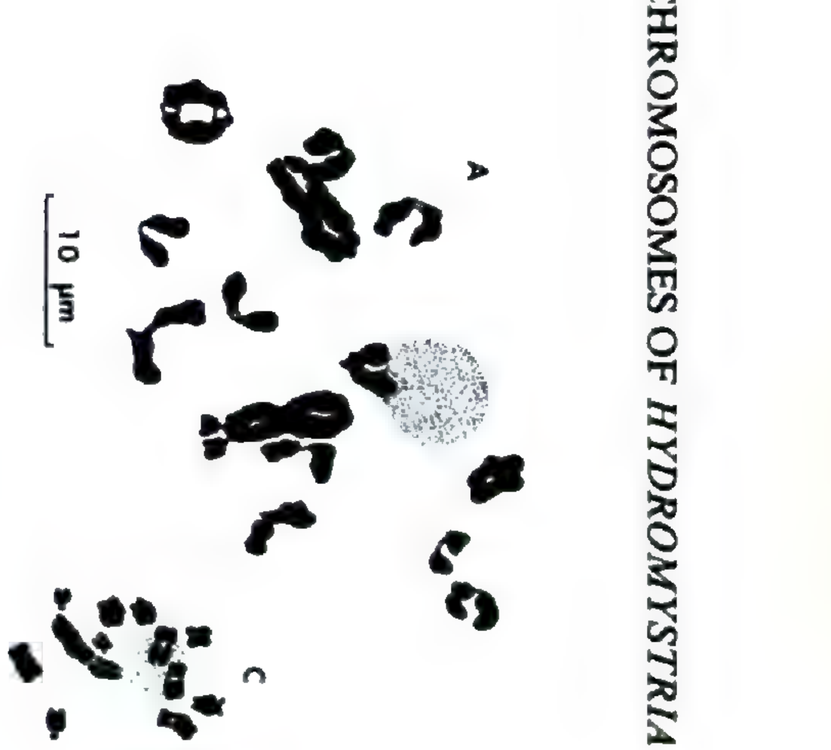

FIGURE 1. *Hydromystria laevigata.*—A. Diakinesis, 14 II (*Moscone et al. 1*).—B. Diakinesis, 14 II (*Bernardello et al. 359 bis*).—C. First mitotic metaphase of pollen grain, $n = 14$ (*Moscone et al. 1*).

Two bivalents much bigger than the others have from two to six chiasmata; they correspond to pairs 1 and 11 from the karyotype, although it is not always possible to distinguish one pair from the other. The remaining bivalents are shorter, similar to each other in length, and generally have only one terminal chiasma. Sometimes they sustain two terminal chiasmata, thus forming ring bivalents. Occasionally, the association of some bivalents to the nucleolus and the first mitotic division of the microspore were observed (Fig. 1C).

Mitotic observations. The somatic chromosome number $2n = 28$ (Fig. 2) was found in 53 metaphase plates of P_1 and 22 of P_2. Based on their arm ratio, the chromosomes can be classified as follows (Fig. 3A, B): 4 *m* pairs (1 to 4), 6 *sm* pairs (5 to 10) and 4 *st* pairs (11 to 14). It should be emphasized that no chromosome is satellited, at least according to our observations. The karyotype is asymmetrical and bimodal.

FIGURE 2. Mitotic metaphases of *Hydromystria laevigata*, $2n = 28$.—A. *Moscone et al. 1.*—B. *Bernardello et al. 359 bis.*

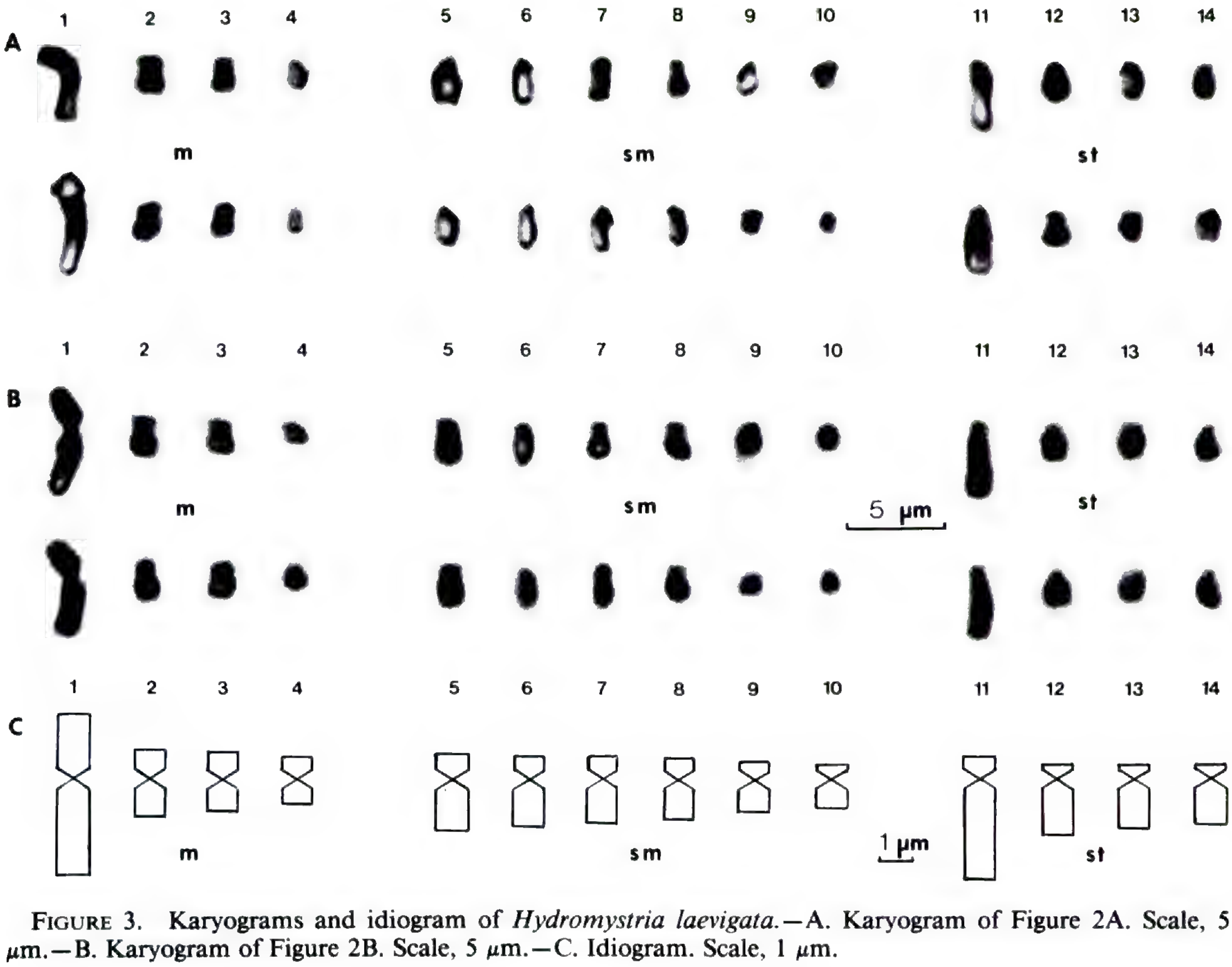

FIGURE 3. Karyograms and idiogram of *Hydromystria laevigata*.—A. Karyogram of Figure 2A. Scale, 5 µm.—B. Karyogram of Figure 2B. Scale, 5 µm.—C. Idiogram. Scale, 1 µm.

Pairs 1 and 11 are considerably larger than the others, which are in general homogeneous in size and thus difficult to characterize. The idiogram (Fig. 3C) was based on chromosome length, data for which are presented in Table 2. Pair 1 is the longest, and pair 10 is the shortest. The lowest arm ratio corresponds to pair 4 and the highest one to pair 11.

DISCUSSION

From the meiotic behavior and the *t*-test results it is evident that both populations have regular meiosis and show no statistical differences in their meiotic systems. Furthermore, the analysis of mitotic chromosomes demonstrates a striking similarity between P_1 and P_2 karyograms although Chaudhuri and Sharma (1978) have mentioned, based on their investigations on *Vallisneria spiralis* L., *Ottelia alismoides* Pers., *Hydrilla verticillata* (L. f.) Royle, and others, the frequent presence of cytotypes in Helobiales. These authors found several cytotypes of those species varying in both chromosome number and morphology. This circumstance has been reported in other members of the Hydrocharitaceae by other botanists (Bhattacharya & Gosh, 1976; Harada, 1956; Misra, 1974; Sharma & Bhattacharyya, 1956).

In contrast to our results, Urmi-König (in Cook & Urmi-König, 1983), studying plants from Guadeloupe, Buenos Aires, and of unknown origin, indicated $2n = 26, 27, 28, 29, 30$ for *H. laevigata* with several chromosome numbers in an individual specimen. Although some differences can be drawn from her karyogram data, it is difficult to compare them because she did not state the terminology used and did not show any figure or photograph. She found one pair of long submetacentric and one medium pair designed as acrocentric. After the widely accepted terminology of Levan et al. (1964), both long pairs are *m* and *sm* according to our results. Urmi-König did not report *sm* chromosomes within the short pairs but did report a number of acrocentric ones.

Geitler (1938) could find neither satellites nor

TABLE 2. Measurements and indexes of somatic chromosomes of *Hydromystria laevigata*. Measurements given in μm. Abbreviations after Levan et al. (1964).

Pair	Chromosome Lengths: Range and Mean ± Standard Error			*r*	i	Nomenclature
	s	l	c			
1	1.72–2.55 2.00 ± 0.092	2.55–4.00 3.06 ± 0.152	4.33–6.55 5.06 ± 0.243	1.53	39.53	m
2	0.80–1.05 0.92 ± 0.028	1.05–1.45 1.21 ± 0.046	1.90–2.50 2.13 ± 0.070	1.32	43.19	m
3	0.73–1.07 0.86 ± 0.036	0.90–1.38 1.09 ± 0.052	1.70–2.45 1.95 ± 0.083	1.27	44.10	m
4	0.60–0.80 0.67 ± 0.019	0.70–0.95 0.77 ± 0.024	1.30–1.75 1.44 ± 0.042	1.15	46.53	m
5	0.68–0.90 0.77 ± 0.024	1.35–2.05 1.61 ± 0.065	2.08–2.90 2.38 ± 0.081	2.09	32.35	sm
6	0.60–0.92 0.69 ± 0.030	1.28–1.83 1.50 ± 0.056	1.90–2.75 2.19 ± 0.078	2.17	31.51	sm
7	0.60–0.80 0.69 ± 0.020	1.15–1.65 1.36 ± 0.051	1.80–2.45 2.05 ± 0.066	1.97	33.66	sm
8	0.57–0.85 0.69 ± 0.027	1.02–1.50 1.22 ± 0.046	1.60–2.35 1.91 ± 0.073	1.77	36.13	sm
9	0.45–0.65 0.52 ± 0.019	0.83–1.15 0.99 ± 0.027	1.30–1.80 1.51 ± 0.043	1.90	34.44	sm
10	0.40–0.58 0.45 ± 0.018	0.80–1.10 0.91 ± 0.029	1.20–1.68 1.36 ± 0.044	2.02	33.09	sm
11	0.60–0.90 0.70 ± 0.030	2.65–4.20 3.10 ± 0.144	3.30–5.10 3.80 ± 0.172	4.43	18.42	st
12	0.35–0.50 0.43 ± 0.019	1.35–2.10 1.63 ± 0.067	1.70–2.60 2.06 ± 0.082	3.79	20.87	st
13	0.37–0.60 0.45 ± 0.021	1.23–1.90 1.49 ± 0.062	1.60–2.50 1.94 ± 0.082	3.31	23.20	st
14	0.37–0.52 0.43 ± 0.016	1.20–1.70 1.39 ± 0.053	1.60–2.20 1.82 ± 0.068	3.23	23.63	st

secondary constrictions in this species. We agree with his observations, although Urmi-König (in Cook & Urmi-König, 1983) reported that one pair bears satellites but without specifying which pair.

Like other Hydrocharitaceae examined (Misra, 1974; Chaudhuri & Sharma, 1978; Bhattacharya & Gosh, 1976; Sharma & Bhattacharyya, 1956) *Hydromystria* has an asymmetrical karyotype.

The basic number of $x = 7$ for *H. laevigata* is one of several previously recorded for the family. The basic numbers, in decreasing order of frequency, are: $x = 8$, 11, 10, 7, and 6 (Fedorov, 1969; Goldblatt, 1981, 1984; Moore, 1973, 1977; Packer & Witkus, 1982).

Some of the genera of Hydrocharitaceae have not been studied cytologically: *Apalanthe, Appertiella, Limnobium* sensu stricto, and *Thalassia,* and the genera *Nechamandra* and *Stratiotes* are insufficiently known. A cytological study of *Limnobium* may help elucidate its relation to *Hydromystria,* on which we are currently working.

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STUDIES IN NEOTROPICAL PALEOBOTANY. III. THE TERTIARY COMMUNITIES OF PANAMA—GEOLOGY OF THE POLLEN-BEARING DEPOSITS[1]

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ABSTRACT

Samples containing fossil pollen and spores were collected from six sites representing five Tertiary formations in Panama. The Gatuncillo Formation is middle(?) to late Eocene, based on foraminifera and mollusk fossils. The formation is exposed around Madden Basin and samples were collected in the vicinity of Alcalde Díaz (Peñoncito). Material from the early Miocene Culebra Formation was obtained from a well drilled in the Contractor's Hill locality at the base of Gold Hill. The Cucaracha Formation overlies the Culebra and is also early Miocene in age. The Cucaracha material was collected from exposures along the Gaillard Cut section of the Canal. The early Miocene La Boca Formation outcrops in the same area. Although these three formations are similar in age (early Miocene), field evidence demonstrates that they are sequential from the Culebra (oldest), through the Cucaracha, to the La Boca (youngest). The Gatun Formation is late Miocene and early Pliocene in age and core samples were taken from a series of wells drilled in Gatun Lake. The location, stratigraphy, lithology, and depositional environments are summarized for these five formations. In subsequent publications the paleocommunities, paleoenvironments, and biogeographic implications will be considered for each of the microfloras.

The present studies on the Cenozoic history of neotropical vegetation began in 1964 with a collection of pollen-bearing samples from Tertiary deposits in central Panama. Subsequently, other samples were obtained from the Oligocene of Puerto Rico and the Miocene of Veracruz, Mexico. At that time the vegetation of Central America was poorly known, but research by staff of the Missouri Botanical Garden, the Field Museum, and various institutions in Central America was rapidly providing new information on the composition of the flora, and on the range, ecology, and biogeographic relationships of its components. By comparison, the vegetation of more restricted areas to the north, such as Puerto Rico and Veracruz, was somewhat better known (Howard, 1973; Gomez-Pompa, 1973), and it seemed logical to begin paleofloristic studies on geologically younger deposits in these areas where modern analogs were more clearly defined. Consequently, our first studies were on the middle Oligocene San Sebastian palynoflora from Puerto Rico (Graham & Jarzen, 1969), followed by the late Miocene Paraje Solo palynoflora from Veracruz, Mexico (Graham, 1976).

The decision to defer consideration of the Panama material was fortunate for several reasons. The older Gatuncillo assemblage from Panama proved the most difficult of our neotropical studies, and recently accumulated information on the modern vegetation was most helpful in making paleoenvironmental reconstructions. The completion of the "Flora of Panama" (1980) and Croat's (1978) "Flora of Barro Colorado Island," initiation of Burger's "Flora Costaricensis," and the "Flora Mesoamerica," coordinated through the Missouri Botanical Garden and Kew, are making both specimens and information available to our studies on vegetational history. Recent biogeographic summaries are also valuable for interpreting the paleofloristic data (e.g., Gentry, 1982). Also, the pollen and spore reference collection, used for identification of the fossil palynomorphs, has increased from 10,000 slides in 1964 to nearly 22,000. From the standpoint of geology, the recently revised "Geologic Map of the Panama Canal and Vicinity, Republic of Panama" (Stewart et al., 1980) and modern plate tectonic summaries (e.g., Coney, 1982; Raven & Axelrod, 1974) are important for placing the paleobotanical data in a sound geologic context.

Pollen-bearing samples from five Tertiary formations were collected in Panama within or adjacent to the former Canal Zone (Figs. 1–3). These

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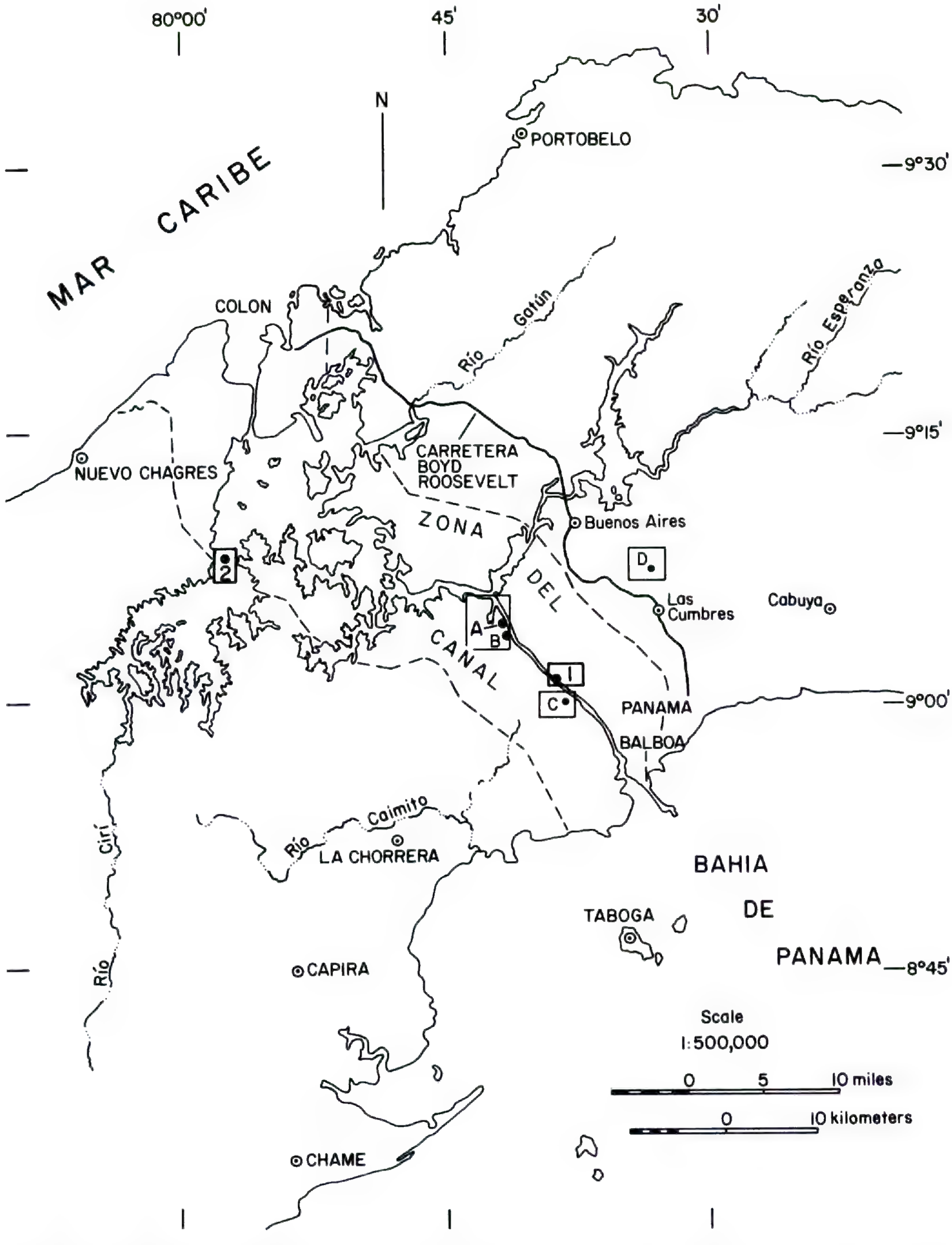


FIGURE 1. Locality map for Tertiary pollen and spore-bearing samples, Republic of Panama.—A, B. La Boca Formation (early Miocene), Las Cascadas Reach of Gaillard Cut, Panama Canal.—C. Cucaracha Formation (early Miocene), Culebra-Cucaracha Reach.—D. Gatuncillo Formation [Middle(?) to late Eocene], near Alcalde Díaz (Peñoncito).—1. Drilling site through the Culebra Formation (early Miocene), Contractor's Hill locality in front of Gold Hill (core GH-9).—2. Drilling site through the Gatun Formation (late Miocene to Pliocene), Gatun Lake (cores SL-48, 49, 60, 103).

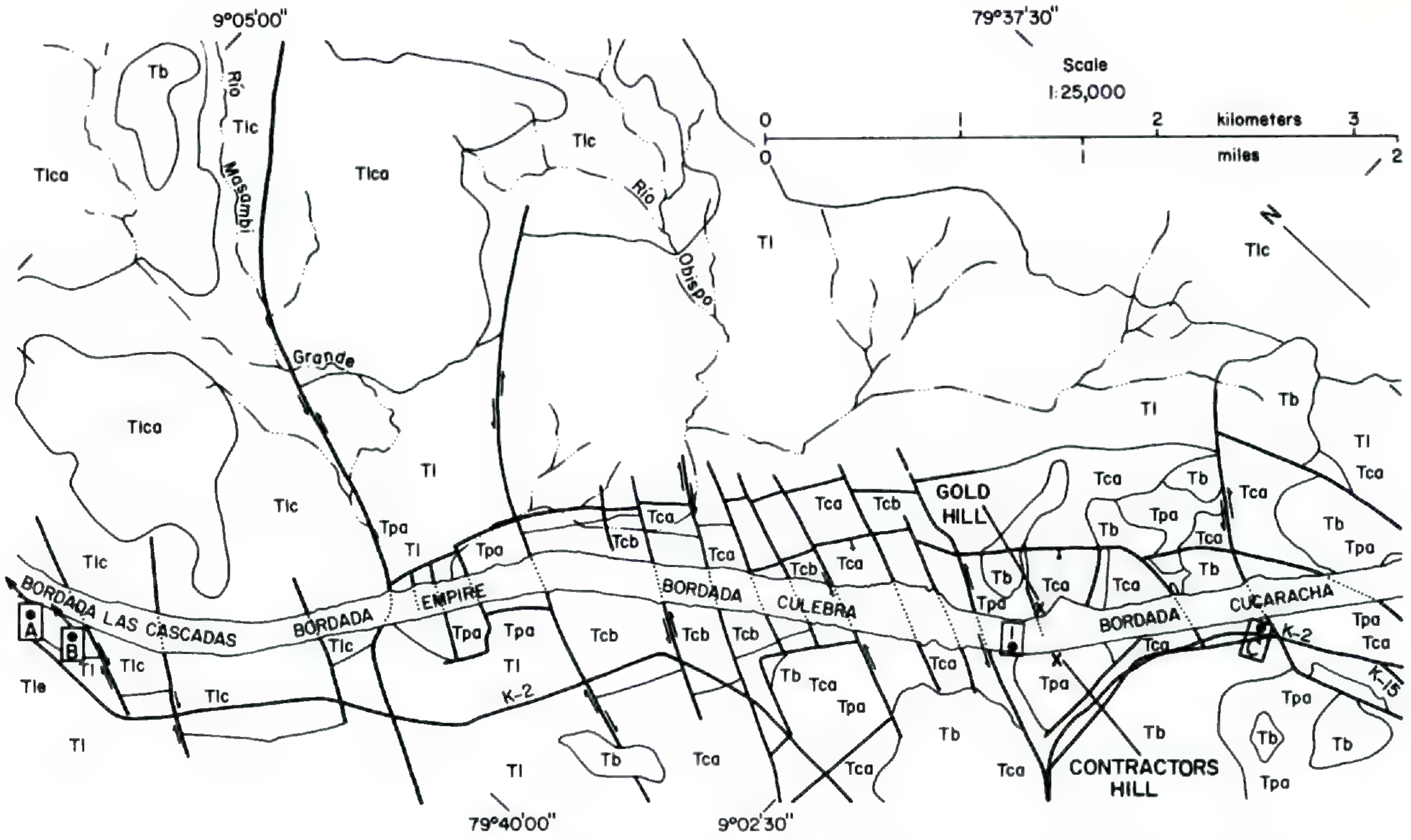


FIGURE 2. Generalized surface geology map, Gaillard Cut section of Canal, Republic of Panama. Collecting sites A and B (La Boca Formation) are along a Canal-facing slope overlain by the Las Cascadas Formation (Tlc), and C (Cucaracha Formation) is overlain in part by the Pedro Miguel Formation (Tpa). Note extensive faulting. Modified from Stewart et al. (1980). Symbols: Tlc—Las Cascadas Formation; Tl—La Boca; Tle—Emperador Limestone member (coralliferous limestone) of La Boca Formation; Tpa—Pedro Miguel; Tcb—Culebra; Tca—Cucaracha; Tlca—andesite, equal in age to Las Cascadas Formation (early Miocene); Tb—intrusive and extrusive basalts (middle and late Miocene).

are the middle(?) to late Eocene Gatuncillo Formation, the early Miocene Culebra, Cucaracha, and La Boca Formations, and the late Miocene to Pliocene Gatun Formation.

The instability of the landscape along the Gaillard Cut, as reflected by the faults shown in Figure 2, presents problems in recognizing the age and stratigraphic relations between the numerous, small, segmented outcrops that are frequently concealed by dense vegetation cover. In addition, special problems arise from maintenance procedures used along the Canal, which often involve removal of vast amounts of slope sediments (Figs. 9–11). This significantly alters the landscape, even between collecting seasons. These procedures are required by the unusual geologic configuration through which the Canal was constructed. During the Tertiary, lava filled many of the valleys and river basins. Subsequent erosion of the softer surrounding sediments below the basalt-filled basins produced a present-day inverted topography in which the modern hills were originally topographic lows. The result is massive, dense basalts resting on top of softer underlying sediments. When the Canal was dug through this mosaic, the weight of the overlying basalts began forcing enormous volumes of sediment into the Canal. The scars from these slippages are a common and characteristic feature of the banks along the Canal. To reduce landslides, the slope face is cut back, and these alterations, combined with the landslides, considerably complicate permanently recording the location and determining the stratigraphic relationships between many of the collecting sites.

The present paper summarizes the geology, depositional environments, and currently accepted ages for five Tertiary formations in Panama from which pollen-bearing samples have been collected. Subsequent studies will trace the history of the vegetation in central Panama as preserved in the palynofloras of the Gatuncillo, Culebra, Cucaracha, La Boca, and Gatun Formations.

THE GATUNCILLO FORMATION

The Gatuncillo Formation was named by Thompson in Panama Canal reports for 1944

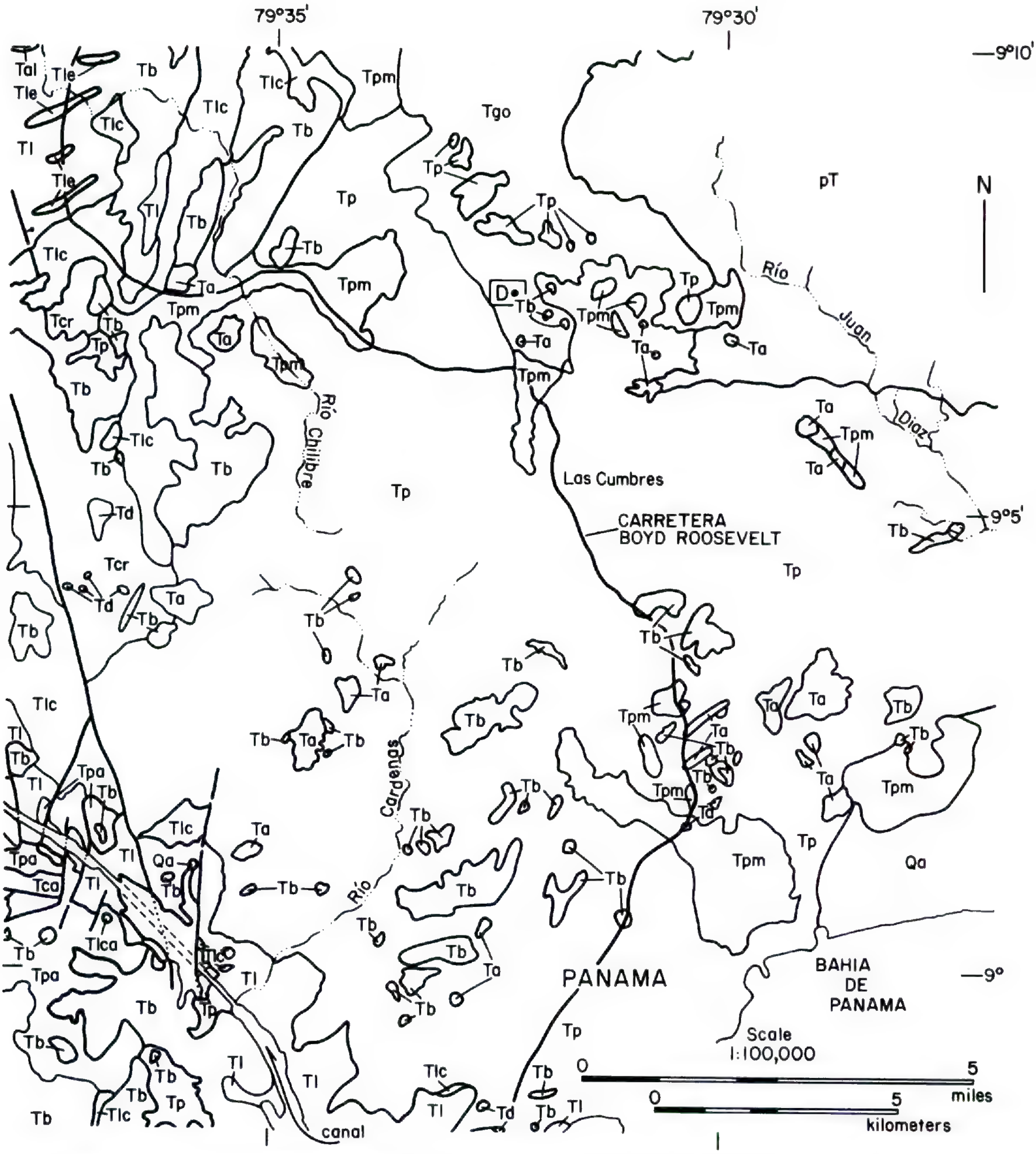


FIGURE 3. Generalized surface geology map, vicinity of Alcalde Díaz [Peñoncito; locality D—Gatuncillo Formation, middle(?) to late Eocene]. Symbols: Tp—Panama Formation (early to late Oligocene); Tpm—Panama (marine facies); Tgo—Gatuncillo; Ta—intrusive and extrusive andesite (Oligocene and early Miocene); Td—intrusive dacite and dacite porphyry (Miocene); Tcr—Caraba (late Oligocene); Qa–Holocene (alluvium or fill). For other symbols see legend to Figure 2.

and first published in Woodring and Thompson (1949). Maximum thickness is about 1,000 m and the formation "unconformably overlies a basement complex of unknown, possibly Cretaceous age consisting of strongly deformed altered volcanics-flows, pyroclastics, and indurated fine-grained sediments that probably were originally fine-grained tuffs" (Woodring & Thompson, 1949: 227).

In the vicinity of our collection sites the formation outcrops around the margins of Madden Basin and Lake Madden north of Panama City (Fig. 3). The Rio Gatun fault terminates the exposure to the north, and the Azota fault defines

portions of its western limits. A few isolated outcrops occur to the west along Gatun Lake and at the north end of Culebra Reach. Elsewhere the formation has been identified in cores to the south as far as Gold Hill and north of Gamboa. In addition, it has been recognized eastward into the Bayano River basin and westward as far as the Costa Rica–Panama border. There are also massive outcrops in the southern part of the Azuero Peninsula.

Local extrusive basalts of Miocene age overlie small areas of the Gatuncillo Formation, and just north of Alcalde Díaz (Peñoncito) there are very local deposits of the Panama Formation forming the tops of hills. The latter is early to late Oligocene in age and composed mainly of agglomerates (andesitic in fine-grained tuff) and stream-deposited conglomerates (an agglomerate is composed of angular volcanic ejecta, in contrast to conglomerate particles rounded by stream transport). The Panama Formation outcrops are rapidly being altered, especially near the former Canal Zone, because these local hilltop deposits are extensively removed for valley fill and road construction.

The Gatuncillo sediments consist of mudstones, siltstones, quartz sandstone, impure bentonite, and coralline and foraminiferal limestone. Interbedded are lenses of lignite ranging from a few centimeters to 1–2 m in thickness. Locally there are overlying deposits of marine limestone. The sequence is typical of nearshore deposition in tropical environments, since lignites presently form under such conditions (Cohen & Spackman, 1972; Scholl, 1964a, 1964b), and those in the Gatuncillo sediments contain *Rhizophora* pollen. The corals fringing the volcanic islands that occupied the region of present-day central Panama during the Eocene, and contributing to the coralline component of the Gatuncillo Formation, further reflect tropical depositional environments. Surrounding most of the Gatuncillo Formation to the east, north, and west are extensive areas mapped as pre-Tertiary. These include altered basaltic and andesitic lavas and tuff, and other dioritic and dacitic intrusives.

Woodring (1957–1982) has made extensive studies on the Tertiary mollusks from the Canal Zone. From the Gatuncillo Formation he reports a fauna most similar to those elsewhere of middle to late Eocene age. Cole (1952) studied the larger foraminifera of the Gatuncillo Formation. He reported 21 species, 18 of which are recorded elsewhere in the late Eocene. The remaining three occur in the middle Eocene, and two of these (*Yaberinella jamaicensis* and *Fabiania cubensis*) are known only from the middle Eocene. Consequently, Cole (1952) refers the Gatuncillo Formation to the middle(?) and late Eocene.

Samples for pollen and spore analysis were obtained from a roadcut section near Alcalde Díaz just off the Boyd-Roosevelt highway (our locality D, Figs. 1, 3–5; samples 1–15; 9°7′N, 79°32′W). The concurrence of the mollusk and foraminifera data, in the absence of any conflicting stratigraphic information, indicates the palynomorphs recovered from the Gatuncillo Formation represent remnants of a middle to late Eocene plant community growing in the region approximately 40 Ma.

The Culebra Formation

The Culebra Formation (Hill, 1898) takes its name from a town located in the central Gaillard Cut during the construction period. The formation outcrops in very limited areas on either side of the Canal along the Gaillard Cut (Fig. 2). Stratigraphic relations are exceedingly complex because of extensive faulting in the area. In a distance of ca. 3 km, more than 113 faults have been observed along Las Cascadas Reach to the north. In one section adjacent to the Canal, along Las Cascadas, Empire, and Culebra Reaches, left-handed fault motions represented in a distance of 4 km total 4 km of displacement.

The Culebra Formation lies unconformably on the Gatuncillo Formation, and has a thickness of about 165 m. It is overlain by the Las Cascadas Formation as revealed by a core (SC-108) drilled at the Las Cascadas Reach (9°04′N, 79°41′W; Canal Station 1615). The Culebra is composed mainly of calcareous sandstones and siltstones, with interbedded lenses of coalified lignite and carbonaceous shales. Like the Gatuncillo Formation, the Culebra also represents a nearshore, transgressive depositional environment and specifically an estuary deposit as evidenced by the very thinly bedded, dark, fine-grained sediments, some of which contain fragments of land plants. In the older literature reference is made to the Empire or Emperador limestone member of the Culebra Formation. This "massive, cream-colored coralliferous limestone, formally exposed in shallow quarries at Empire, was named the Empire limestone by Hill (1898: 195–196). Empire, now abandoned, was a village on the original line of the Panama Railroad near Culebra and about half a mile west of Gaillard Cut"

4

FIGURES 4, 5. Roadside exposure of the middle(?) to Late Eocene Gatuncillo Formation near Alcalde Díaz (9°7′N, 79°32′W; locality D), Republic of Panama (January 25, 1983).—4. General view showing basal lignite and overlying siltstone.—5. Close-up of lignite area shown in lower-left corner of Figure 4.

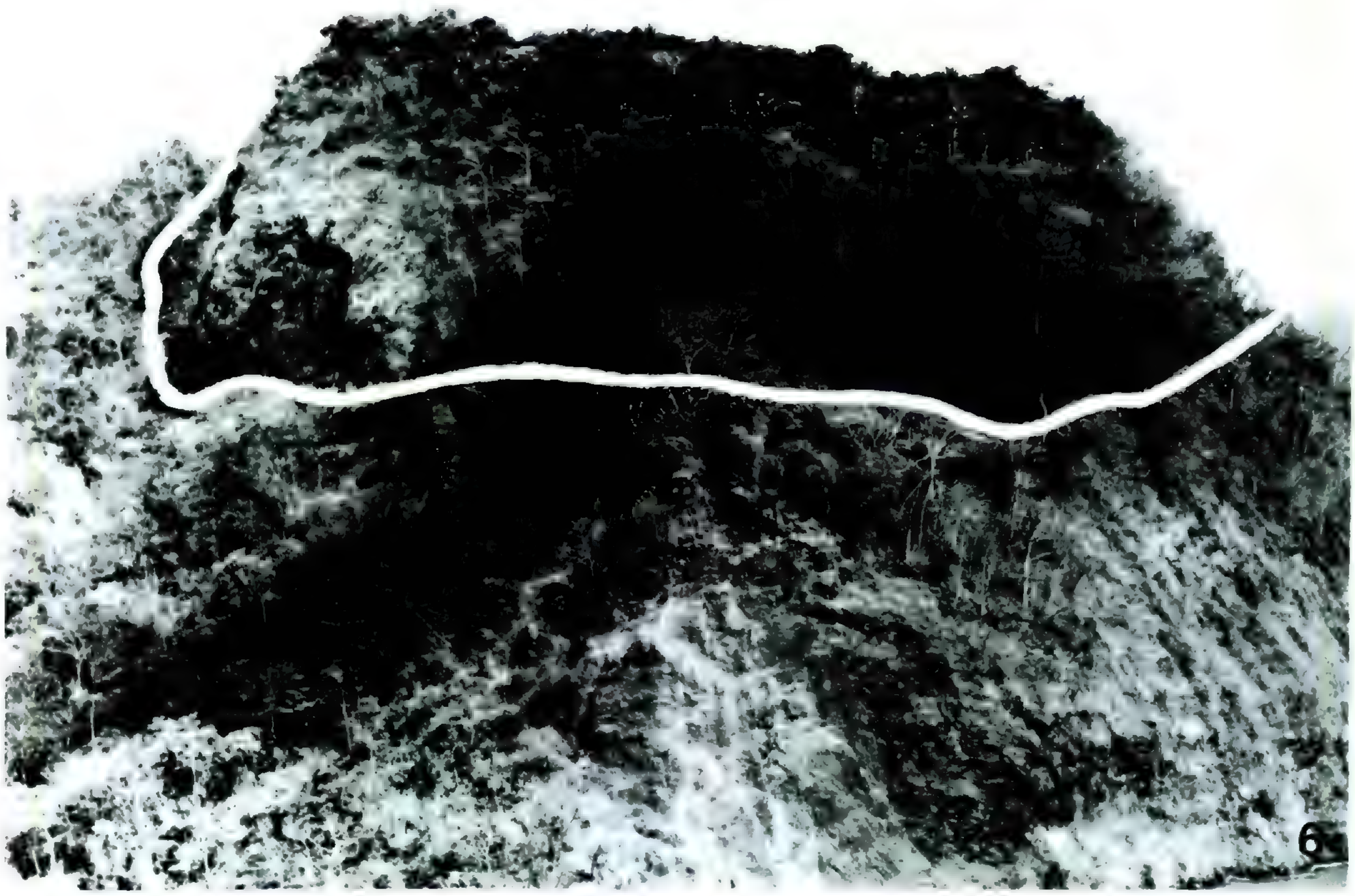


FIGURE 6. The southwest face of Gold Hill on the Gaillard Cut section of the Canal, Republic of Panama. Core material from the lower Miocene Culebra Formation was obtained from a well drilled in front of Gold Hill on the west side of the Canal (9°02′N, 79°38′W; drill site 1 on Fig. 1). The subsurface stratigraphy for the Culebra Formation at this site is summarized in Tables 1 and 2 from the well log data. The line separates an unnamed basalt of late Miocene or early Pliocene age (above) from upper lower Miocene agglomerates of the Pedro Miguel Formation (below).

(Woodring & Thompson, 1949: 237). The Emperador is now included as a member within the lower La Boca Formation.

Woodring (1957–1982) assigns the Culebra to the lower Miocene based on mollusk data. Stratigraphic relations with overlying fossiliferous deposits, and one tentative potassium-argon date from the Cucaracha Formation (see below), further suggest a lower Miocene age. In previous stratigraphic columns (e.g., Woodring & Thompson, 1949), the Culebra Formation was assigned to the upper Oligocene.

A well was drilled through the Culebra Formation (locality 1 on Fig. 1) that provided fossiliferous samples and log data detailing the subsurface stratigraphy of the formation. The well was completed on January 8, 1958 and the field log was filed with the Engineering and Construction Bureau of the Panama Canal Commission. Subsequently the cores were discarded, but copies of the logs, unprocessed samples, vials of processed material, and slides are preserved in the palynology collections at Kent State University.

The samples were obtained from Hole No. GH-9; latitude 9°02′N + 2912.3, longitude 79°38′W + 5561.5; ground elevation 29.6 m (+96.1 ft.); core recovery 124 m (402.6 ft.; 80.5%) from a total section of 154 m (500.2 ft.); project—Gold Hill Investigation; location—in front of Gold Hill on the west side of the Canal and in front of the Model Slope which is just north of Contractor's Hill (Fig. 6). Fifty-seven samples were taken along the 124 m section (Table 1), primarily from carbonaceous layers within the predominantly sandstone section (labeled in our collections as PAN Core, Culebra Formation). From these, 21 samples were processed and all contained fossil pollen and spores. The stratigraphy and lithology for portions of the core sampled are given in Table 2.

THE CUCARACHA FORMATION

The Cucaracha Formation outcrops on both sides of the Canal from Hodges Hill southward to the area of Pedro Miguel Locks. The most

TABLE 1. Samples from Panama Canal Company's Hole No. GH-9, Contractor's Hill locality, Culebra Formation (lower Miocene), Republic of Panama. Figures represent depth in feet along the core. Arrangement of the samples is subdivided according to core box sequence used by the PCC. Although these boxes and samples have been discarded, the sequence is still referred to in the summary section of the Geological Field Log of the Contractor's Hill locality, Gold Hill Investigation.

Box 12 of 17	Box 13 of 17	Box 14 of 17	Box 15 of 17	Box 16 of 17
370.2[a]	392	424	446.7	474
376.5[a]	394.3	424.6	448[a]	476
377[a]	407[a]	425[a]	449.4	479
378.4[a]	409	427.5	450	481
382[a]	411	428.6	451	482.5
383	412.6	433.3	452[a]	483.6
385.7	415.5[a]	435	454.6	486
388.7		437.9[a]	456[a]	488[a]
		438.6	459.6	490.6[a]
		440.7	461[a]	491[a]
		441.9	463.4[a]	491.6[a]
		442.9[a]	466	494
		444.6	469.8[a]	494.9
			470.6[a]	495.8
				496.8

[a] Samples from which fossil pollen and spores have been recovered.

prominent and accessible outcrops are on the southwestern side of the Cucaracha Reach sector of the Gaillard Cut between Canal Stationing 1983 and 2010. The formation is named after a railroad station and a small town that existed prior to Canal construction.

The Cucaracha Formation is composed mostly of bentonitic clay shales, tuffaceous siltstones, and sandstones with discontinuous lenses of lignite and freshwater conglomerates. The total thickness of the Cucaracha Formation is about 183 m. The formation is divided into an upper and a lower zone. A layer of ash flow or ignimbrite divides the two zones.

The upper part consists of the following: clay shales over siltstone, an upper lignite bed ca. 0.5 m thick, a clay shale, a conglomerate ca. 0.5 m thick, a lower lignite bed ca. 0.5 m thick, a clay shale, and the ash flow at the base. The dip of the beds is 15°, and the dip of the slope is about 20°. The lignites range from a black, friable, fissile, lignite shale to a coalified lignite. All of these beds in the upper part are in fault contact with the basalt in the upper part of the hill.

The ash flow or ignimbrite is a layer of volcanic debris 8 m thick with tentative potassium-argon dates of 22.2 ± 1.7 and 18.9 ± 2.2 Ma (Woodring, 1982: 551).

The lower 0.5 m of the ash flow contains numerous carbonized logs, twigs, and roots. In places, the old stumps were found still upright with roots extending into the strata below. This zone represents an old forest layer that was carbonized and buried by an explosive volcanic eruption. Immediately to the north of the area, just north of Contractor's Hill at the Model Slope, 75% of the log bases exposed during Canal widening excavations pointed north and northeasterly indicating the direction from which the eruption came.

The 100 m of strata below the ash flow consists primarily of alternating, recurrent layers of clay shale, tuffaceous siltstone, tuffaceous sandstone, and conglomerate with scattered layers of lignitic shale. This sequence is repeated many times throughout the lower part of the section. At the base of the section is a basal conglomerate containing abundant oysters, indicating a nearshore depositional environment. Occasional well-worn specimens of *Miogypsina cushmani* can be found in some of the upper layers of sandstone. These were likely derived from nearby outcrops of the Culebra Formation that had been uplifted by tectonic activity prior to the deposition of this part of the Cucaracha Formation.

The dominant plant is a coarse grass, *Saccharum spontaneum* L., introduced from the Old World tropics and now widespread throughout the Canal area. On fresh exposures this grass initially aligns itself along the lignite outcrops (Fig. 8) and is a convenient marker for these organic-rich sediments. Later, as the grass spreads and slumping of the sediments occurs, this relationship is obscured.

Along road K-2 about 0.8 km northwest of the intersection with K-15 in the Gaillard Cut section of the Canal is a roadside exposure of the Cucaracha Formation (our locality C, samples 57a–66, Figs. 1, 2, 7, 8). Across the road on the Canal side the ash flow continues and the lower 1.5 m includes highly decomposed logs representing the forest layer at this site. Below the tuff is another clay shale, then a 0.7 m lignite near water level that is not evident on the roadside section. This lignite rests on a clay shale with 25 cm diameter siderite ($FeCO_3$) concretions.

At this locality there is a small utility building adjacent to a power pole (Fig. 7). About 4 m

TABLE 2. Stratigraphy and lithology of samples from the Culebra (lower Miocene) Formation, Republic of Panama. Representative data selected from Panama Canal Company's Geological Field Log, Hole No. GH-9, Contractor's Hill locality, Gold Hill Investigation.

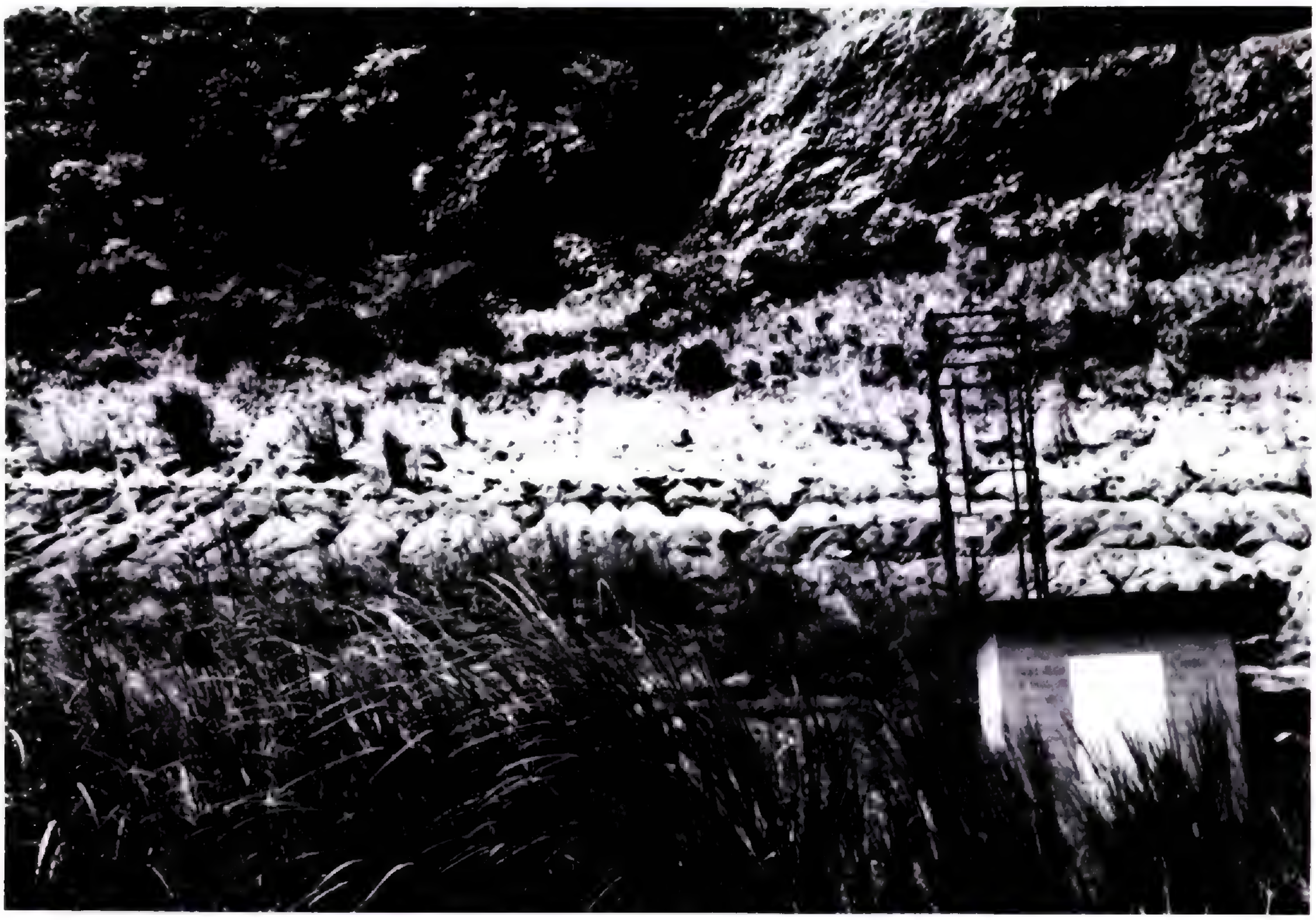
Elevation (ft.)	Depth (ft.)	Descripton of Material	Core Recovery
−270.2	366.3	SANDSTONE, RH 1–2, moderately soft to medium hard, moderate strength, moderate jointing, very thin bedding, medium to coarse grained, variably calcareous and carbonaceous, fossiliferous; color: mottled medium and dark grays. NOTE: thin, highly carbonaceous layers make innumerable dark gray lines.	26.9 (90.5%)
−299.9	396.0	SANDSTONE, RH 1–2, moderately soft to medium hard, moderate strength, moderate jointing, very thin bedding, medium to coarse grained, variably calcareous and carbonaceous, fossiliferous; color: mottled medium and dark grays. NOTE: thin, highly carbonaceous layers make innumerable dark gray lines.	49.4 (92.5%)
−353.3	449.4	SANDSTONE, RH 1–2, soft to medium hard, moderate strength, moderate jointing, very thin bedding; fine to medium grained with very high silt content; variably calcareous, carbonaceous, and fossiliferous; color: mottled medium and dark gray; thin carbonaceous layers make innumerable dark gray lines.	
−404.1	500.2	SANDSTONE, RH 1–2, soft to medium hard, moderate strength, moderate jointing, very thin bedding; fine to medium grained with very high silt content; variably calcareous, carbonaceous, and fossiliferous; color: mottled medium and dark gray; thin carbonaceous layers make innumerable dark gray lines. Bottom of hole.	50.0 (98.4%)

above and to the left of the pole is a conspicuous conglomerate layer 1 m thick. The conglomerate terminates abruptly and continues on the other side of the pole about 4 m down in the section. This displacement is 9 m of left lateral motion, and the fault is one of the hundreds that characterize the Gaillard Cut section of the Canal. All samples were collected to the right of the fault line (facing the slope), and no faults were observed through the section sampled.

About 0.7 km further to the right (NW) is part of the locality from which Whitmore and Stewart (1965) reported fossil mammal bones, all belonging to a fauna with distinct northern affinities. The collecting sites of the mammal bones extended from Canal Station 1994 in the north to Canal Station 2011 in the south. This site also contains large numbers of presumably crocodilian coprolites. Several of these were collected and processed, but the palynomorphs were poorly preserved and in low concentrations. In this distance of ca. 0.7 km, two faults intervene, and, although the mammal beds are altitudinally equivalent to the layers sampled for fossil palynomorphs, they are stratigraphically lower. Clearly, sampling in this complex region must take into account the unusually large number of faults, frequently obscured by slumping and dense vegetation, that occur within very short distances.

A well was drilled near this site on October 4, 1958 (Hole No. PA-33; latitude 9°01′N + 5914.9, longitude 79°38′W + 2300.0; ground elevation 56 m (+182.7 ft.); core recovery 40.8 m (132.5 ft.; 71.4%); project—Cucaracha Reach Widening Studies; location—Cucaracha Reach). The drilling logs are filed with the Panama Canal Commission, and copies are in the palynology collections at Kent State University. Relevant portions of the log are summarized in Table 3. It is noted that only 71.4% of the core was recovered, and among the missing strata are the conglomerate layer and the lower roadside lignite described earlier. The initial lignite referred to in the log is the uppermost layer in the roadside section.

The general sedimentology of the section, and the sequence of lithologies, reveal the overall nature of the depositional environment. Lignites form under coastal, brackish water conditions where slow-flowing rivers empty onto a relatively broad coastal plain and where a dense vege-



FIGURES 7, 8. Exposures of the Cucaracha Formation (locality C) along the banks of the Canal, Republic of Panama.—7. Alternating layers of dark lignites and lighter ash and conglomerates.—8. Lignite layer with 15–20 cm thick overburden of eroded ash and lignite. Note the horizontal alignment of the grass *Saccharum spontaneum* L. along the lignite zone.

TABLE 3. Stratigraphy and lithology of samples from the Cucaracha (lower Miocene) Formation, Republic of Panama. Representative data selected from Panama Canal Company's Geological Field Log, Hole No. PA-33, Cucaracha Reach locality.

Elevation (ft.)	Depth (ft.)	Description of Material	Core Recovery
+111.2	71.5	LIGNITIC SHALE, RH-1, soft, weak, closely jointed, thin bedded; contains an abundance of carbonaceous plant debris; color: dark gray to black. (This is the uppermost lignite layer described from the roadside exposure from which fossil pollen-bearing samples were collected.)	1.7 (100%)
+109.5	73.2	CLAY SHALE, RH-1, soft, weak, very closely jointed with joints highly slickensided; consists of a fine-grained, water-laid volcanic tuff highly altered to montmorillonite and bentonitic clay minerals; color: medium gray-green. (Note that only 53% of the core was recovered; missing is the conglomerate and basal lignite layer described from the roadside section.)	6.8 (53%)
+102.7	80.0	ASH FLOW, RH-3, hard, strong, moderate jointing, massive bedding, fine-grained, porphyritic, agglomeratic; consists of a dacitic ignimbrite; color: purple, greenish gray, and brown. (This is the layer from which the K-Ar date was obtained; the lower 2 feet represent the old forest layer.)	19.2 (80%)
+85.0 (Canal water level)	97.7		
+78.7	104.0	CLAY SHALE, RH-1, soft, weak, very closely jointed and slickensided, thinly bedded; consists of a fine-grained volcanic tuff highly altered to montmorillonite and bentonitic clay minerals; silt content increases with depth; color: gray-green.	48.3 (37%)
+35.0 (Bottom of canal)	147.7		
+30.4	152.3	LIGNITIC SHALE, RH-1, soft, weak, closely jointed, thinly bedded, contains an abundance of carbonaceous plant debris; color: dark gray to black. (This is the layer on the Canal side of the road below the lowermost layer on the roadcut exposure.)	2.0 (83%)
+28.0	154.7	CLAY SHALE, RH-1, soft, weak, very closely jointed and slickensided, thinly bedded; consists of a fine-grained volcanic tuff highly altered to montmorillonite and bentonitic clay minerals; variably silty and sandy; contains some calcareous concretions in upper portion; color: 157.4 to 165.6, gray-green, 165.6 to 172.9, gray-green mottled with red-brown, 172.9 to 184.4, red-brown, 184.4 to 185.6, gray-green mottled with red-brown. NOTE: Some scattered calcareous concretions in red-brown layer from 180.6 to 181.4 ft. depth (these are the siderite concretions discussed previously).	28.6 (93%)
−2.9	185.6	Bottom of hole.	

tation (frequently dominated by mangroves) and moderate off-shore currents allow organic detritus to accumulate. Climatic conditions under which modern lignites are presently forming are warm-temperate, subtropical to tropical (Cohen & Spackman, 1972; Scholl, 1964a, 1964b). The shoreline was periodically inundated, probably from local subsidence of the land rather than changes in sea level, as evidenced by the folding and faulting of the strata. The clays and silts contain both marine invertebrates and debris from land vegetation. Extensive volcanism is documented by the tuffs (water-lain volcanic ash) and the basalt that caps the section.

THE LA BOCA FORMATION

The La Boca Formation outcrops along both sides of the Canal from the Pacific entrance to Las Cascadas Reach. It is composed of mudstones, siltstones, sandstones, lignited shales, tuffs, and limestones. The Emperador limestone is a

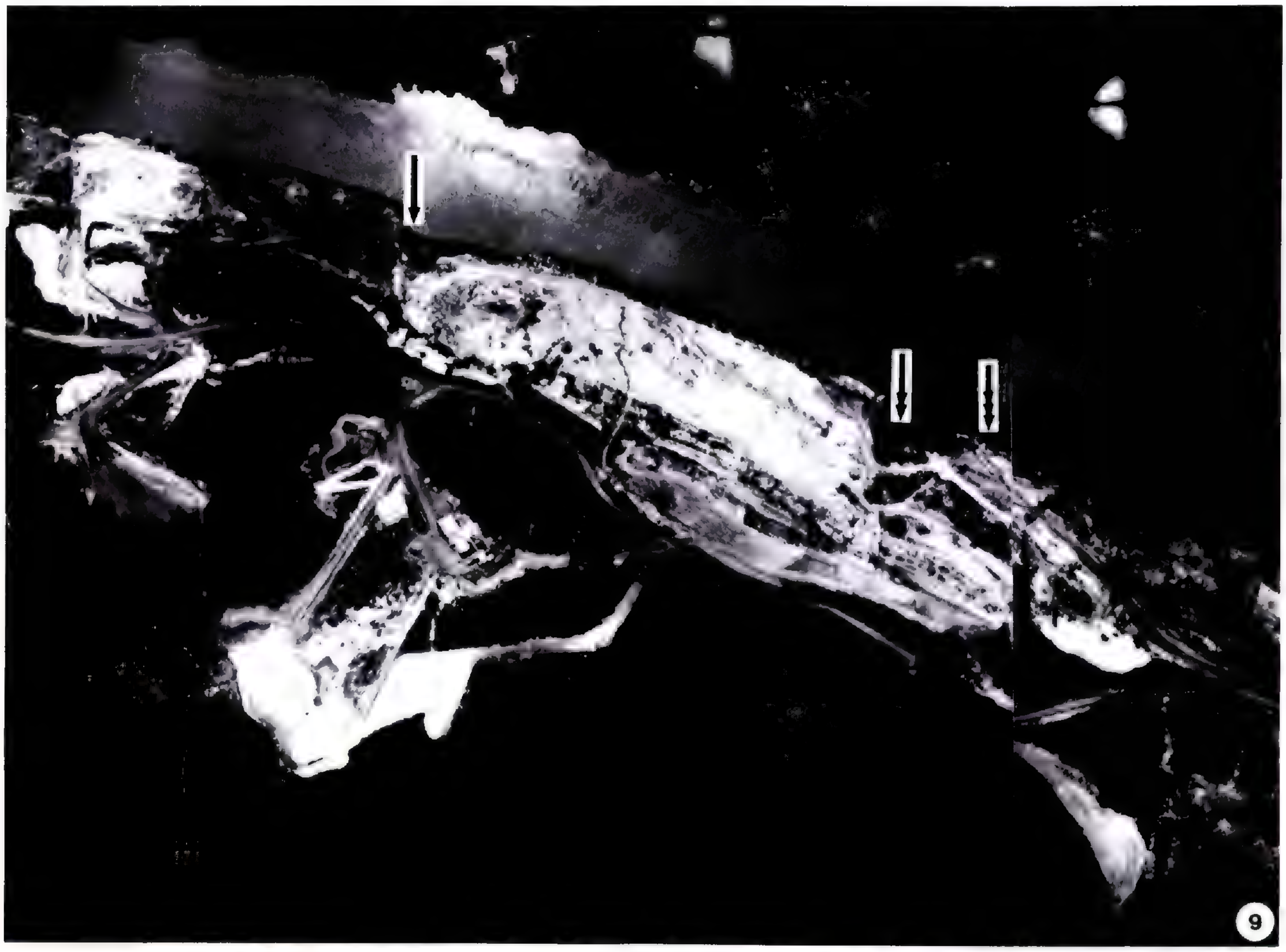


FIGURE 9. Aerial photograph of Las Cascadas Reach of the Canal, Republic of Panama, 1967, when this section was being widened from 90 m to 155 m. Single arrow designates collecting locality A in the early Miocene La Boca Formation at canal marker 1600 (1766 new system). Double arrow designates drilling site LBW-88 through the La Boca Formation at canal marker 1619 (1785 new system; 9°04′N, 79°40′W; log data summarized in Table 5). Triple arrow designates collecting locality B in the La Boca Formation at canal marker 1622 (1788 new system). Other samples were collected at markers 1625 (1791) and 1627 (1793) further to the right.

member of the lower part of the La Boca composed of coralliferous limestone reflecting warm, subtropical to tropical marine environments. These conditions are consistent with the layers of lignite that occur throughout the lower part of the section (see previous discussion, Cucaracha Formation). The sequence of sediments indicates a period of subsidence with bathyl siltstones (Blacut & Kleinpell, 1969) capping the section. The lignitic layers contain shells of marine invertebrates and substantial amounts of pyrite resulting from the oxidation of soluble ferrous compounds by iron bacteria. Woodring (1982) recognized 130 species of mollusks from the La Boca and their collective ranges suggest an early Miocene age.

In September 1967, samples were collected from two Canal-side exposures of the La Boca Formation (Fig. 2). Our locality A (samples 1–26) was on the Las Cascadas Reach at station marker 1600 (1766 new stationing), and locality B (samples 27–54) was at markers 1622 (1788), 1625 (1791), and 1627 (1793). At that time the Canal was being widened from 90 m to 155 m (Figs. 9–11), and by the January 1983 field season this construction was complete. Thus, compared to the present physiography, the 1967 samples were collected from strata 25 m up and 60 m out over the Canal. The beds dipped back into the slope 20–25° so that now the same lignite layers are nearly at water level and, in this area, near the La Boca–Las Cascadas contact (Fig. 12).

In addition to these challenging alterations in the landscape, the Canal marking system has changed. Marker number 1625 (in our 1967 collections) is now 1791. This complicates any study dealing with the former Canal Zone and vicinity where canal markers were used as reference points. The Panama Canal Commission has a list correlating the new and old numbers, and

FIGURES 10, 11. Exposures of the La Boca Formation at locality A, Las Cascadas Reach of the Canal, Republic of Panama, in 1967 during widening of the Canal [near canal marker 1600 (1766 new system); see Figure 9].—10. General view of the locality.—11. La Boca Formation. Note the fault abruptly terminating the white tuff at the lower left of the exposure. Over 113 of these faults have been mapped in a distance of 3 km in the Gaillard Cut section of the Canal.

TABLE 4. List correlating the old collecting site numbers to the new collecting site numbers. From the Panama Canal Commission.

1967 Stationing	Present Stationing
1600	1766
1619	1785
1620	1786
1622	1788
1625	1791
1627	1793

those pertaining to our collecting sites are summarized in Table 4.

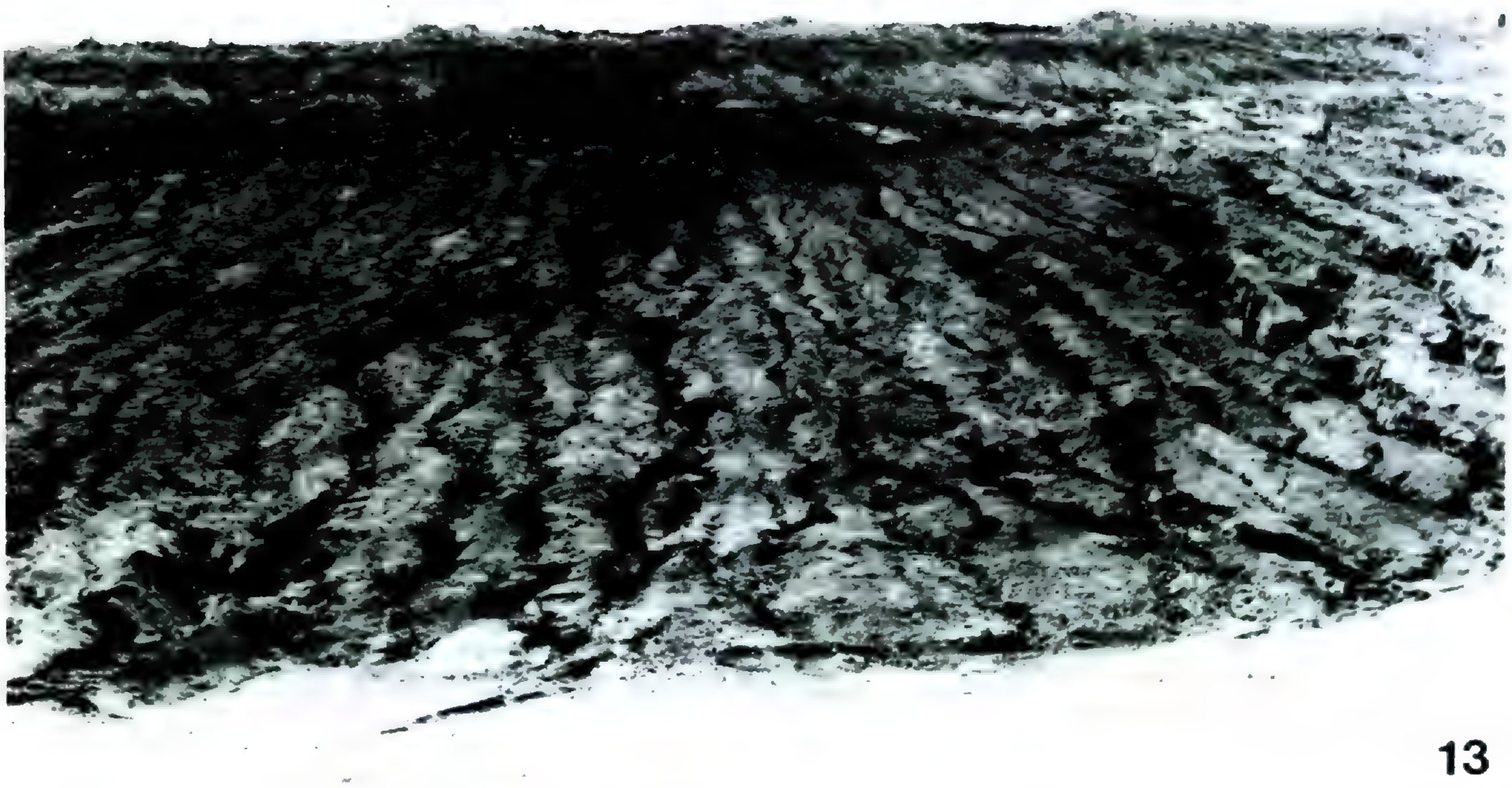
It should also be noted that reference points may be cited on North American datum or Canal Zone datum. To change North American to Canal Zone datum, add 941 ft. to longitude and 942 ft. to latitude; to change Canal Zone to North American datum, substract 941 ft. from longitude and 942 ft. from latitude. Latitudes and longitudes cited in this study are on North American datum.

On April 6, 1960, a well was completed at canal marker 1619 (old system; 1785 new stationing) near our collecting sites. The log provides general information on the stratigraphy and lithology of the La Boca Formation [Hole No. LBW-88; latitude 9°04′N + 4586.4, longitude 79°40′W + 4557.1; ground elevation 52.7 m (+171.4 ft.); core recovery 38 m (123.5 ft.; 72.0%); project—Canal Improvement; location—Las Cascadas Reach; old station 1619, 1785 new stationing]. The logs are filed with the Engineering and Construction Bureau of the Panama Canal Commission, and copies are in the palynology collections at Kent State University. The relevant portions of this log are summarized in Table 5.

It is evident that the Culebra, Cucaracha, and La Boca Formations are similar in age (lower Miocene), and that stratigraphic relations are complicated by the highly faulted and altered nature of the sediments along the Gaillard Cut. Another source of earlier confusion resulted from an inadvertent coring error in the 1950s that led to incorrect correlations in some major paleon-

TABLE 5. Stratigraphy and lithology of samples from the La Boca (lower Miocene) Formation, Republic of Panama. Representative data selected from Panama Canal Company's Geological Field Log, Hole No. LBW-88, Las Cascadas Reach locality (station 1619).

Elevation (ft.)	Depth (ft.)	Description of Material	Core Recovery
+48.0	123.4	LIGNITIC SHALE, soft rock, closely jointed, joints slickensided, thin bedding; contains abundant carbonaceous plant debris and some marine borings filled with fossiliferous material; color: dark gray to black.	1.5 (57%)
+45.9	126.0	SILTSTONE, soft rock, thin bedding, moderate jointing with joints slickensided, fossiliferous at base; color: medium gray-green.	3.5 (77%)
+40.9	130.5	LIGNITIC SHALE, soft rock, closely jointed, joints slickensided, thin bedding; contains abundant carbonaceous plant debris and some marine borings filled with fossiliferous material; color: dark gray to black.	0.0 (0%)
+38.4	133.0	SILTSTONE, soft rock, thin bedding, moderate jointing with joints slickensided, fossiliferous at base; color: medium gray-green.	0.9 (45%)
+36.4	135.0	LIGNITIC SHALE, soft rock, closely jointed, joints slickensided, thin bedding; contains abundant carbonaceous plant debris and some marine borings filled with fossiliferous material; color: dark gray to black.	0.5 (16%)
+33.4	138.0	AGGLOMERATE, tuffaceous, soft rock, moderate jointing with joints open; some joints recemented with calcite and zeolite; massive bedding; consists of andesitic and basaltic pebbles and cobbles in a fine-grained, tuffaceous matrix of similar composition; some fragments are pumaceous; somewhat altered to various clay minerals and chlorite; material checks rapidly on exposure to air and falls apart; color: mottled grays and light greens. NOTE: Very tuffaceous in lower 11.0 ft., almost a tuff.	25.9 (77%)
−0.1	171.5	Bottom of hole.	



FIGURES 12, 13. 12. New exposures of lower Miocene La Boca lignites (January 1983), Republic of Panama, after 61.5 m widening project started in 1967 was completed (see Figs. 9–11). This is locality B, and when samples were collected in 1967 the slope face was 25 m up and 60 m out over the Canal. Since the beds dip back at an angle of ca. 20–25°, the lignite bed (base of the figure) is now at water level.—13. Contact between the La Boca (marine phase) to the left (south) of the figure (R. S. Stewart) and the Las Cascadas (terrestrial volcanic) to the right (north; January 1983). La Boca is documented younger than Las Cascadas because it is on top, even though beds are vertical through uplift and left-lateral faulting. Slumping has obscured lithological differences between the formations at the contact (canal marker 1909).

TABLE 6. Location of pollen-bearing samples from the upper Miocene and Pliocene Gatun Formation and other Cenozoic deposits, Republic of Panama. Cores are designated by the Panama Canal Commission's system, and samples from each core are listed according to depth in feet (except HU's SL-60 sample at 40 ft. which is at a depth of ca. 127 ft.). Samples were collected in December 1962, by Elso Barghoorn and Alexandra Bartlett (HU), or in December 1963, by A. G. (KSU). All slides are presently in the palynology collections at KSU.

KSU	HU	
Core SL-48 (Latitude 9°11′ + 1331; Longitude 79°55′ + 4501)		
157		Gatuncillo
158		
162	162	
Core SL-49 (Latitude 9°08′ + 4113; Longitude 79°57′ + 1987)		
222.5		Gatun
223		
223.5		
Core SL-60 (Latitude 9°11′ + 6042; Longitude 79°52′ + 411)		
	40	Caimito Formation
Core SL-103 (Latitude 9°16′ + 5945; Longitude 79°52′ + 2963)		
	178	Quaternary
	250	Gatun
	253	
255.5		
257		

tological publications dealing with the Culebra and La Boca Formations. Van den Bold (1972, 1973) correlated the La Boca with the Culebra based on ostracod data and similarities in lithology. The same correlation was made by Woodring (1957) from mollusk evidence. R. H. Stewart (pers. comm.) found field evidence that was inconsistent with this correlation (see below) and re-examined the core from which the invertebrate fossils had been obtained. Stewart discovered that a piece of Cucaracha material from previous drillings had stuck in the core barrel and worked loose in the next drilling which was through the La Boca. Woodring (1982) subsequently corrected the error for the mollusk studies.

Field stratigraphy reveals that the three formations are sequential within the early Miocene from the Culebra (oldest) through the Cucaracha, to the La Boca (youngest). This stratigraphy, used on the most recent version of the geologic map of Panama (Stewart et al., 1980), is based on the observation that in local areas the Cucaracha Formation sits on top of the Culebra. Above the Cucaracha is another formation, the Pedro Miguel. The terrestrial phase of the La Boca has not been observed directly on the Cucaracha, but it does interfinger with the Pedro Miguel, and therefore must be younger than the Cucaracha. In addition, the marine phase of the La Boca does rest directly on the Las Cascadas Formation (Fig. 13) which is the same radiometric age as the Cucaracha Formation. Thus, the Culebra, Cucaracha, and La Boca Formations, as presently understood, represent a time-stratigraphic sequence for the early Miocene in central Pan-

TABLE 7. Summary of log data for four cores through Tertiary and Quaternary formations in Panama from which fossil pollen and spores were recovered. Depth and elevation are in feet. See Table 6, Figure 1 (locality 2), and text for location of drilling sites.

Core	Elevation	Depth	Description of Material
SL-48	+86.5	0.0	Water
	+6.5	80.0	Overburden
	−64.9	151.4	Top of weathered rock (samples SL-48, 157, 158, 162) SILTSTONE, medium hard to hard (OH 3–4); slightly to medium plastic; medium tough to tough; medium to high dry strength; clayey with streaks weathered to clay; slightly sandy, with very fine sand; color: mottled, gray and brown. (Gatuncillo Formation.) Recovery 10.4 ft.
	−76.6	163.1	Top of sound rock SILTSTONE, medium hard (RH-2); massively jointed, no joints apparent; core in 0.1 ft. and smaller pieces broken during drilling by dry blocking;

TABLE 7. Continued.

Core	Elevation	Depth	Description of Material
			slightly sandy with fine sand; fairly clayey and marly; massively bedded, no bedding apparent; color: dark gray to gray. (Gatuncillo Formation.) Recovery 1.2 ft.
	−77.8	164.3	Final depth
SL-49	+86.9	0.0	Water
	+14.9	72.0	Overburden
	−133.2	220.1	Top of sound rock (samples SL-49, 222.5, 223, 223.5)
			SILTSTONE, soft to medium hard (RH 1–2); massively jointed, no joints apparent; core in one piece 4.6 ft. long and in 0.1 ft. and smaller pieces, broken during drilling by dry blocking; slightly sandy with fine sand; fairly clayey; quite marly with scattered white streaks of shell fragments; massively bedded, no bedding apparent; friable; color: dark gray. (Gatun Formation.) Recovery 4.7 ft.
	−138.9	225.8	Final depth
SL-60	+87	0.0	Water
	+6	81.0	Overburden
			SILT, CLAY, AND ORGANIC MATERIAL, laid down since formation of Gatun Lake.
	−1.0	88.0	GRAVEL AND SILT.
	−4.7	91.7	SILT AND CLAY, soft to medium soft (OH 1–2); loose; medium plastic; slightly spongy at plastic limit, friable below plastic limit; very weak; low dry strength; sticky, high water content, and containing many carbonaceous wood fragments; color: dark gray and black. (Atlantic Muck.) Recovery 32.2 ft.
	−40.3	127.3	Top of weathered rock (sample SL-60, 40)
			SANDSTONE, medium hard to very hard (OH 3–5); jointing apparent at base only; silty; bedding not apparent; color: gray-green and brown. (Weathered Caimito Formation.) Recovery 9.8 ft.
	−60.0	147.0	Top of sound rock
			SANDSTONE, medium hard to hard (RH 2–3); closely jointed; core recovered in poor condition in 0.01–0.4 ft. lengths with 0.1 ft. lengths and fragments predominant; medium grained, silty, with occasional calcareous lenses near the base; bedding where apparent inclined about 5°; color: light gray-green with calcareous lenses almost white. (Caimito Formation.) Recovery 6.18 ft.
	−99.3	186.3	Final depth
SL-103	+85.7	0.0	Water
	+47.7	38.0	Fill
	+17.4	68.3	Overburden (sample SL-103, 178)
	−163.3	249.0	Top of weathered rock (samples SL-103, 250, 253)
			SANDSTONE, hard (OH-5 to RH-1), silty; locally clayey; scattered streaks of light blue-gray clay; slightly waxy locally; checks upon drying; color: dark gray; grades into underlying sound rock. (Weathered Gatun Formation.)
	−168.4	254.1	Top of sound rock (samples SL-103, 255.5, 257)
			SANDSTONE, soft to medium hard (RH 1–2); massively jointed; medium grained; silty; carbonaceous; fossiliferous; contains scattered small pyrite grains; dark gray and greenish gray; core recovered in 0.5–2 ft. lengths. (Gatun Formation.) Recovery 10 ft.
	−178.4	264.1	Final depth

ama. These strata provide a rare opportunity in tropical paleobotany to study the vegetational history of a single region through a defined segment of Tertiary time.

THE GATUN FORMATION

The Gatun Formation was named by Howe (1907: 113–114) from the type region extending from the bluff overlooking Gatun Lake near Gatun, northward to Mount Hope, formerly known as Monkey Hill, near Colon (Woodring & Thompson, 1949). Surface outcrops are extensive on the north (Caribbean) side of the Canal bordering the northern shore of Lake Gatun. The rocks are sandstone, siltstone, tuff, and conglomerates typical of nearshore deposition. The Gatun Formation is relatively unfaulted, whereas the nearby Eocene, Oligocene, and lower Miocene formations are heavily faulted. Thus, the stratigraphic position and geomorphology indicate a post lower Miocene age, although the Gatun Formation has not been observed in the field to rest directly on any of these. The Gatun Formation does rest with a strong, angular unconformity on the pre-Tertiary, Cretaceous volcanics and sediments. There are ash flows or pumice beds within the Gatun sediments that may eventually provide radiometric dates.

The upper part of the Gatun Formation is distinctly marine. Foraminifera from offshore, presumed Gatun sediments (DSDP, R. H. Stewart, pers. comm.), contain some Pliocene species, and Vokes (1983) believes, on the basis of other invertebrates, that the Gatun could be as young as basal Pliocene. Near the Refineria Panama, Colon, a small knoll is composed almost exclusively of shells of marine invertebrates, especially *Turitella*. Woodring (1957–1982) has made extensive studies of mollusks from this and other Gatun localities, and these provide another basis for estimating the age of the formation. A total of 339 species have been described, and collectively they were interpreted to suggest a middle Miocene age. This assignment is used on the most recent version of the geologic map of Panama (Stewart et al., 1980). More recently, however, R. H. Stewart (pers. comm.) believes that a reassessment of the paleontological evidence, combined with observations on the stratigraphy, suggests that the Gatun Formation may be upper Miocene and Pliocene in age. A preliminary survey of the pollen and spores reveals an assemblage quite modern in aspect, and, for purposes of our studies, we are now tentatively accepting the younger age assignment.

In 1962 the Panama Canal Commission drilled a series of wells in Gatun Lake to test the foundation for new water storage construction as part of the Trinidad Dam studies. The upper portions of these cores penetrated pollen-bearing post-glacial sediments and were used by Bartlett and Barghoorn (1973) for their study of Quaternary vegetational history and sea-level changes in Panama. The lower portions of the cores that penetrated surface Gatun Formation sediments also contained a rich pollen and spore flora. It is fortunate that samples from the cores were obtained because all surface exposures are marine and none are known to contain plant microfossils. Samples containing fossil pollen and spores are listed in Table 6, and the location of the drilling site is indicated as locality 2 on Figure 1. Relevant log data from the cores are summarized in Table 7.

In the preceding sections the age, stratigraphic relationships, lithology, and depositional environments are summarized for five pollen/spore-bearing Tertiary formations in Panama. Attention is devoted to the original location of collecting sites; alteration in the landscape that has affected these formations; noting changes in the Canal marking system and datum reference points that can confuse comparison with previously published studies; noting errors in earlier correlations; and recording the permanent location of unpublished well logs, samples, processed material, and slides in the palynology collections at Kent State University.

The rationale for providing these details in an introductory paper is three-fold. First, it is convenient to integrate geological information on the several formations in a single publication. Second, it is possible that these lignite beds will be further altered or destroyed through construction activities along the Canal, or rendered no longer accessible because of political changes affecting Central America. For example, the core material used by Bartlett and Barghoorn (1973) for their study of Quaternary vegetational history in Panama, previously housed in storage facilities of the Panama Canal Commission, has been destroyed. The Tertiary portions of these cores, including all core material mentioned in this paper, measuring hundreds of thousands of feet and containing vast amounts of irretrievable information on the biology and geology of Panama,

were also discarded. Fortunately, samples were obtained in 1964 and 1967, and these constitute a major part of the present study. Finally, individuals now in residence in Panama (R. H. Stewart and J. L. Stewart) and other life-long students of Central American paleontology (e.g., W. P. Woodring) will soon be altering these direct associations with Panama. Their cooperation in facilitating almost every recent paleontological investigation within the Canal Zone is widely recognized, together with their impressive knowledge of local field geology and the extensive unpublished literature. Consequently, it seems timely to initiate these studies on the Tertiary history of vegetation in Panama with a revised summary of the geology of the formations.

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STUDIES IN NEOTROPICAL PALEOBOTANY. IV. THE EOCENE COMMUNITIES OF PANAMA[1]

ALAN GRAHAM[2]

ABSTRACT

The middle(?) to upper Eocene Gatuncillo Formation outcrops near Alcalde Díaz, Panama. From layers of lignite in the formation an assemblage of fossil pollen and spores was recovered, including *Selaginella, Ceratopteris, Pteris,* monolete fern spores (Types 1–5), trilete fern spores (Types 1–5), cf. *Tillandsia,* Palmae (Types 1–5), cf. *Campnosperma, Ilex,* cf. Araliaceae, cf. *Paragonia/Arrabidaea,* cf. *Protium,* cf. *Tetragastris, Combretum/Terminalia, Casearia, Lisianthius,* cf. *Tontalea, Alfaroa/Engelhardia* (rare), *Crudia,* Malpighiaceae, cf. *Ficus, Eugenia/Myrcia, Coccoloba, Rhizophora, Faramea* and other Rubiaceae, *Cardiospermum, Serjania, Paullinia,* cf. *Chrysophyllum, Pelliceria,* and *Mortoniodendron.* Moist lowland communities, as presently occur between the Atlantic side of Gatun Lake and Piña, are well represented, whereas vegetation of higher altitudes and drier habitats is poorly represented or absent. A reconstruction of paleoenvironments, based on varied lines of biological and geological evidence, includes a series of volcanic islands of moderate to low relief, bordered seaward by shallow limestone-depositing coralline communities, and fringed by mangrove swamps of *Rhizophora* and especially *Pelliceria.* Inland communities included tropical moist, tropical wet, and premontane wet forests growing under the general tropical conditions of high rainfall (ca. 2,500 mm) and high uniform temperatures. The lowland insular environment may not record subtle climatic changes more evident in paleocommunities derived from continental areas of greater topographic relief and may reflect paleoenvironmental conditions in the immediate vicinity of the Gatuncillo depositional basin. An assessment of regional paleoclimates and paleophysiography must await discovery of other fossil floras, because the Gatuncillo assemblage is the only one of Eocene age known for northern Latin America.

The vegetation characterizing the Eocene epoch in northern Latin America is completely unknown. There has never been a detailed study published on an extensive flora of this age for Central America, Mexico, or the Antilles. Consequently, the Gatuncillo palynoflora of Panama is of interest in providing a first view of this vegetation. The nearest Eocene fossil floras to the south are from the upper Los Cuervos and Mirador Formations of Colombia (Gonzalez Guzman, 1967) and the Rio Turbio Formation of Argentina (Romero, 1977; for a more complete bibliography see Graham, 1973a, 1979a, 1982). The former are of early and middle Eocene age, compared to the late Eocene Gatuncillo palynoflora, and the latter presently treats only the gymnosperms and the Fagaceae. Both belong to a completely different paleophysiographic province because at this time South America was isolated between Africa and North America (e.g., Raven & Axelrod, 1974), while the present region of Central America was occupied by a series of volcanic islands trailing south from the North American continent (Coney, 1982; Dengo, 1973).

To the north the closest Eocene floras are from the Mississippi Embayment and Gulf coast region studied by Dilcher and collaborators (e.g., Dilcher, 1973), Elsik (1974), Frederiksen (1980), and others. These are some 2,500 km from the Panama localities. Additional information is provided by Germeraad et al. (1968), Muller (1981), and Graham (1977), but these are either preliminary reports or deal with the fossil record of specific palynomorphs rather than entire palynofloras. The results presented here are considered an initial effort to characterize the Eocene vegetation of central Panama and must be augmented considerably before a detailed concept of the regional paleocommunities, paleoenvironments, and vegetational history can be developed.

THE COLLECTING LOCALITY

Samples were collected from a roadside exposure of the Gatuncillo Formation near Alcalde Díaz (Peñoncito). The area is shown on the Alcalde Díaz quadrangle map (sheet 4243 II NE,

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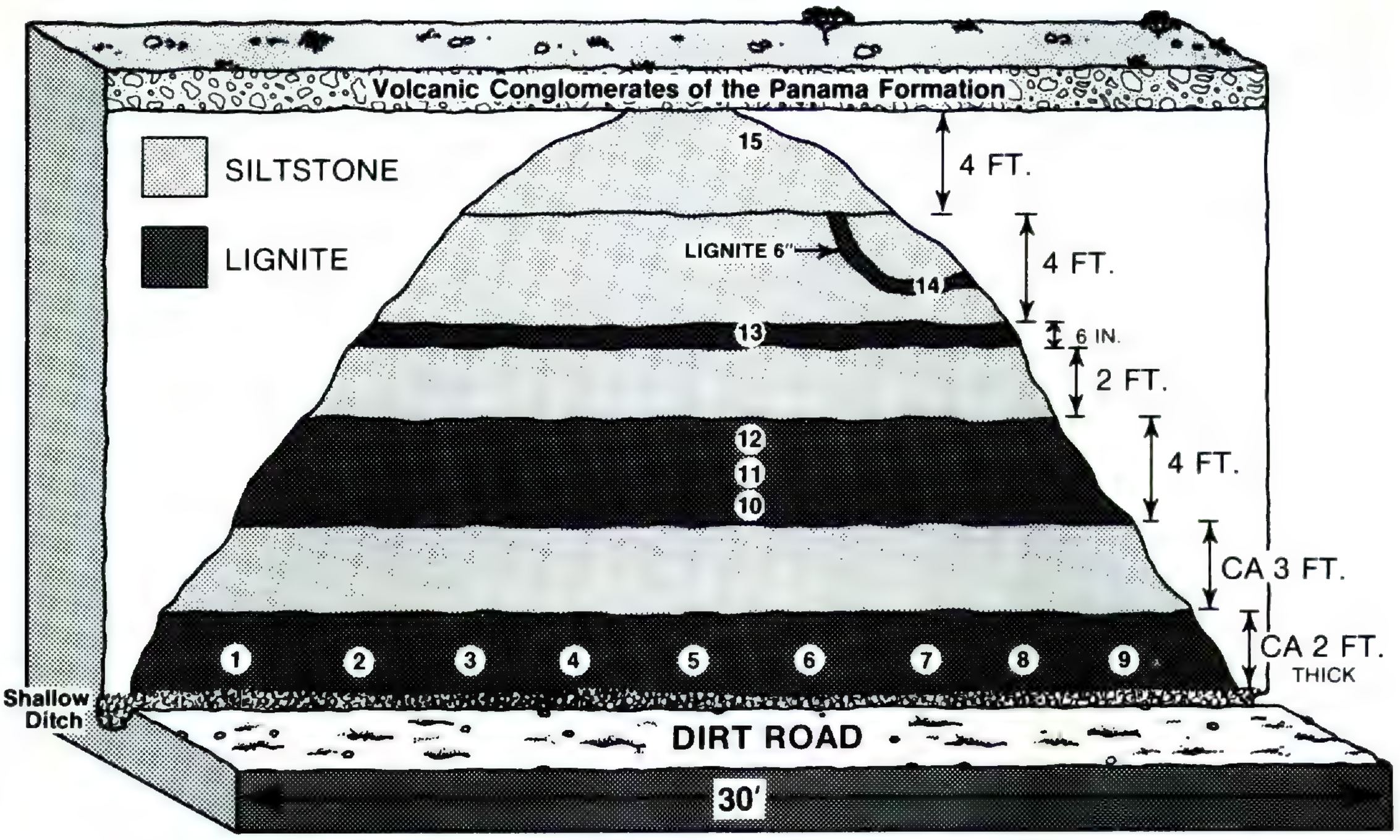


FIGURE 1. Diagrammatic section through roadcut exposure of the Gatuncillo Formation near Alcalde Díaz, Panama (see Graham et al., 1985 for discussion of the locality).

Series E866, scale 1:25,000) prepared by the Army Map Service, Corps of Engineers at coordinates 9°7′N, 79°32′W (North American datum). The site is reached from Panama City by the Boyd-Roosevelt Highway. About 1.8 km from Las Cumbres a dirt road departs to the right. The locality is along this road 2.2 km from the highway intersection.

This site is designated as our locality D and in January 1967, 15 samples were collected (Fig. 1). The beds are tilted at an angle of about 30°. Samples 1–9 are from a basal lignite ca. 0.6 m (2 ft.) thick. This layer is overlain successively by a 0.9 m (3 ft.) siltstone, a second lignite 1.2 m (4 ft.) in thickness (samples 10–12), a 0.6 m (2 ft.) siltstone, a 150 cm (6 in.) lignite (sample 13), a 1.2 m (4 ft.) siltstone with a thin lignite lens (sample 14), and a 1.2 m (4 ft.) siltstone (sample 15) separated from the underlying siltstone by a thin erosion surface. The section is capped by early to late Oligocene conglomerates of the Panama Formation. A visit to the locality in January 1983 revealed that considerable slumping had taken place and the exposure was covered by a nearly uniform veneer of silt 300–460 cm (12–18 in.) thick with a dense overgrowth of herbaceous vegetation (mainly grasses) beginning to develop.

From among the samples, numbers 2, 4, and 9 (all from the lower lignite) yielded the most well-preserved and abundant palynomorphs, and the present study is based primarily on these samples. Slides from the other lignites and the uppermost siltstone were also examined, however, and contained essentially the same microflora. Thus the data base for this study is somewhat limited but not restricted to the microfossils from the lower lignite.

Woodring (1957–1982) has studied the mollusks of the Gatuncillo Formation, and Cole (1952) studied the larger foraminifera. On the basis of the stratigraphic distribution of these fossils in other Caribbean deposits, both authors conclude the Gatuncillo is middle(?) to late Eocene in age. The possibility of a middle Eocene age is considered because three of the larger foraminifera are known elsewhere in strata of this age, and two (*Yaberinella jamaicensis* and *Fabiania cubensis*) are known only from the middle Eocene.

In addition to the lignites and mudstones/siltstones, the Gatuncillo in surrounding areas includes quartz sandstones and coralline and foraminiferal limestones. This lithology reflects deposition in a nearshore coastal environment, and the lignites specifically indicate warm-tem-

TABLE 1. Identification and numerical representation of fossil palynomorphs from the Eocene Gatuncillo Formation, Panama. Figures are percentages based on counts of 200.

	Sample 2	Sample 4	Sample 9
Selaginellaceae			
Selaginella	2.5	—	4
Parkiaceae			
Ceratopteris	—	—	15
Polypodiaceae			
Pteris	0.5	—	—
Trilete Fern Spores			
Type 1	2	—	—
Type 2	—	—	—
Type 3	2.5	0.5	—
Type 4	—	—	—
Type 5	4	1.5	—
Monolete Fern Spores			
Type 1	5	1.5	2
Type 2	1	—	1
Type 3	0.5	—	—
Type 4	—	—	—
Type 5	—	—	—
Bromeliaceae			
cf. *Tillandsia* Type 1	0.5	1	—
cf. *Tillandsia* Type 2	—	—	—
Palmae			
Type 1	—	—	—
Type 2	—	2	—
Type 3	0.5	0.5	—
Type 4	4	2	3
Type 5	3	1.5	1.5
Anacardiaceae			
cf. *Campnosperma*	—	1	1.5
Aquifoliaceae			
Ilex	—	1	2
cf. Araliaceae	—	6	—
Bignoniaceae			
cf. *Paragonia/Arrabidaea*	—	1	—
Burseraceae			
cf. *Tetragastris*	—	—	—
cf. *Protium*	—	—	1.5
Combretaceae			
Combretum/Terminalia	—	3	1.5
Flacourtiaceae			
Casearia	—	—	—
Gentianaceae			
Lisianthius	0.5	2.5	—
Hippocrateaceae			
cf. *Tontalea*	—	—	1
Juglandaceae			
Alfaroa/Engelhardia	—	—	—
Leguminosae/Caesalpinioideae			
Crudia	0.5	3.5	—
Malpighiaceae			
Type 1	—	—	—
Type 2	—	0.5	2
Moraceae			
cf. *Ficus*	—	0.5	0.5
Myrtaceae			
Eugenia/Myrcia	—	0.5	1
Polygonaceae			
Coccoloba	—	3.5	2
Rhizophoraceae			
Rhizophora	9	6	10
Rubiaceae			
Faramea	0.5	—	2
Type 1	—	4	1.5
Type 2	—	3.5	1
Sapindaceae			
Cardiospermum	—	—	—
Paullinia	—	0.5	—
Serjania	—	—	—
Sapotaceae			
cf. *Chrysophyllum*	—	—	2
Theaceae			
Pelliceria	0.5	7	11
Tiliaceae			
Mortoniodendron	1	0.5	—
Unknown Echinate Types			
Type 1	—	—	—
Type 2	—	—	—
Type 3	—	—	—
Type 4	—	—	—
Type 5	—	—	—
Unknown Intectate Type			
Type 6	0.5	—	0.5
Unknown Triangular Type			
Type 7	—	—	1.5
Unknown Oblate/Oblate-Spheroidal Types			
Type 8	—	—	—
Type 9	—	—	—
Type 10	—	—	0.5
Type 11	—	—	—
Type 12	2.5	2.5	—
Type 13	—	—	—
Type 14	—	—	1
Type 15	—	—	—
Type 16	—	—	—

TABLE 1. Continued.

	Sample 2	Sample 4	Sample 9
Type 17	1	1.5	1
Type 18	2.5	2	—
Type 19	1	—	—
Type 20	—	—	—
Type 21	—	—	—
Unknown Prolate, Tricol(por)ate Types			
Type 22	4.5	5	3.5
Type 23	1.5	—	1
Type 24	3.5	1.5	—
Type 25	—	2	—
Type 26	5.5	3	—
Type 27	3	3	2
Type 28	4	2.5	0.5
Type 29	—	—	—
Type 30	6.5	4	2
Type 31	5.5	0.5	1
Type 32	—	0.5	—
Type 33	—	0.5	—
Type 34	0.5	0.5	—
Type 35	—	2	—
Type 36	2.5	2	—
Type 37	1.5	0.5	—
Type 38	—	—	1
Type 39	—	—	—
Type 40	—	—	—
Other Unknowns	14	11.5	17.5

perate to tropical conditions (Cohen & Spackman, 1972; Scholl, 1964a, 1964b). Other details on the geology of the Gatuncillo Formation are summarized by Graham et al. (1985).

MATERIALS AND METHODS

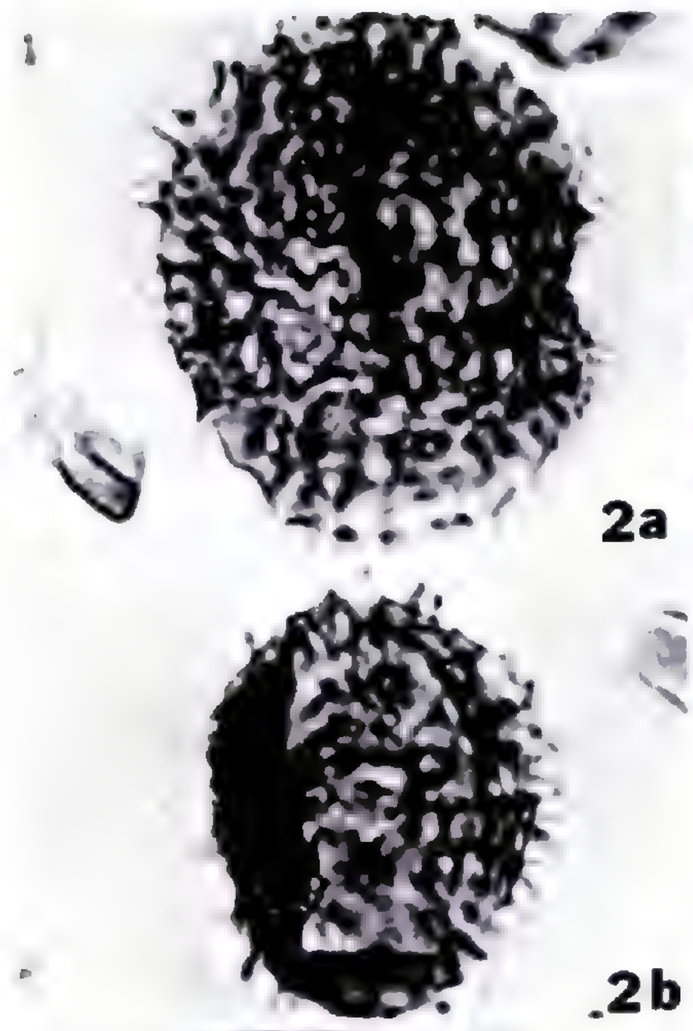
Samples were prepared by cleaning the surfaces to remove contaminants and palynomorphs damaged by oxidation. Pieces of lignite between two and three grams were broken in a mortar and pestle and covered with 10% HCl to remove carbonates. The samples were then passed through HF (to remove silicates), nitric acid (to oxidize lignins and other organic debris), and 10% KOH. Residues were mounted unstained in glycerine jelly and sealed with CoverBond. Photographs were taken with a Zeiss photomicroscope using Panatomic X film. Location of palynomorphs on the slides is indicated by England Slide Finder coordinates. All materials from the study are deposited in the palynology collections at Kent State University.

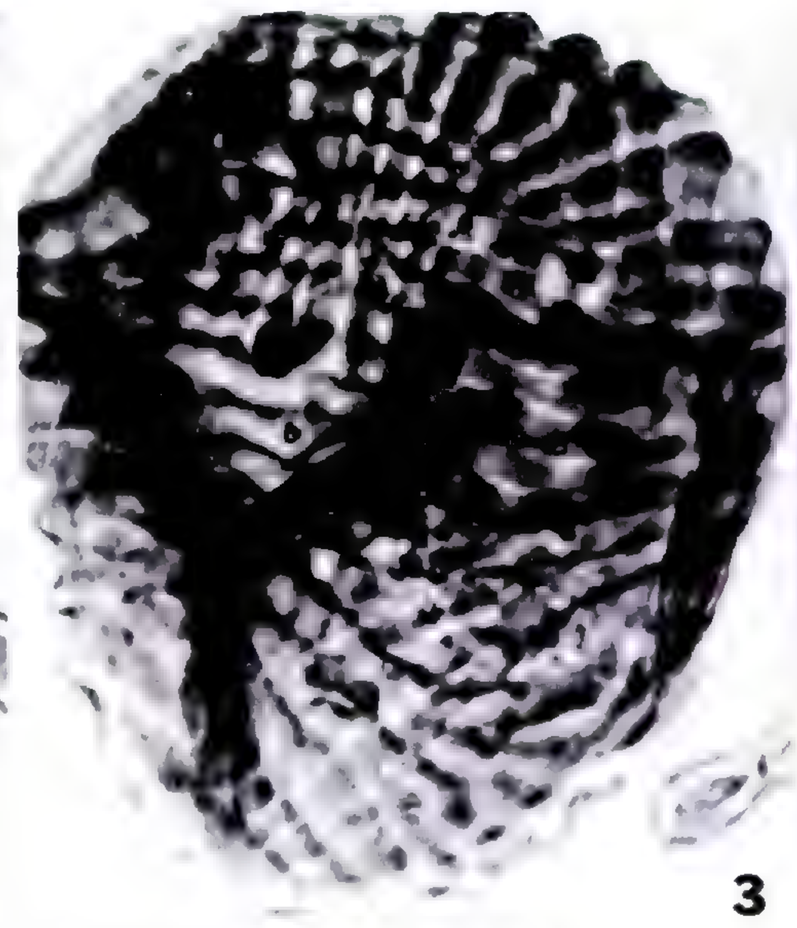
SYSTEMATICS

A total of 47 palynomorphs were identified from the Gatuncillo Formation, and 40 other morphological types were recovered whose biological affinities are unknown (Table 1). The prefix cf. designates the identification is probable, but not as certain as those referred to specific taxa. This is usually due to minor quantitative differences between the modern and fossil pollen or spore that could be the consequence of preservation, or reflect the age difference between the Eocene specimens and their presumed modern analogs. In other instances the specimens may be similar both to a common neotropical genus, and to a taxon from some remote geographic region, characteristic of a completely different biozone (e.g., northern boreal), a rare species, or a plant with exceptionally low pollen production and a highly specific entomophilous pollinating mechanism. Although it may be likely the specimens represent the pollen-prolific, common neotropical genus, it is theoretically possible they represent the other form. The cf. designation is also useful in providing examples of morphologically similar pollen to augment the discription and illustration of the fossil specimen (for a more specific example of identification procedures see cf. *Tillandsia* Type 2).

Identification of the microfossils is based on comparisons with taxa in a modern pollen and spore reference collection numbering about 22,000 slides (ca. 20,000 species). To minimize bias in the identifications towards present-day Panamanian or Central American vegetation, our preparations include species from throughout Latin America (Mexico, the Antilles, Central and South America). In addition, exchanges are maintained with some 20 other laboratories throughout the world. Pollen and spore floras, and published results of other paleopalynological studies on Cenozoic deposits in various regions, are also consulted. Consequently, the possibility of bias in the identification of the microfossils towards a given geographic region or a particular community is recognized and is not regarded as a major problem considering the broad coverage of the reference collection and the available literature.

In the pollen descriptions below, sculpture patterns are described as seen under light microscope (LM) magnifications of about 430–970×. In some instances a sculpture pattern appearing as faintly scabrate under LM may be revealed as

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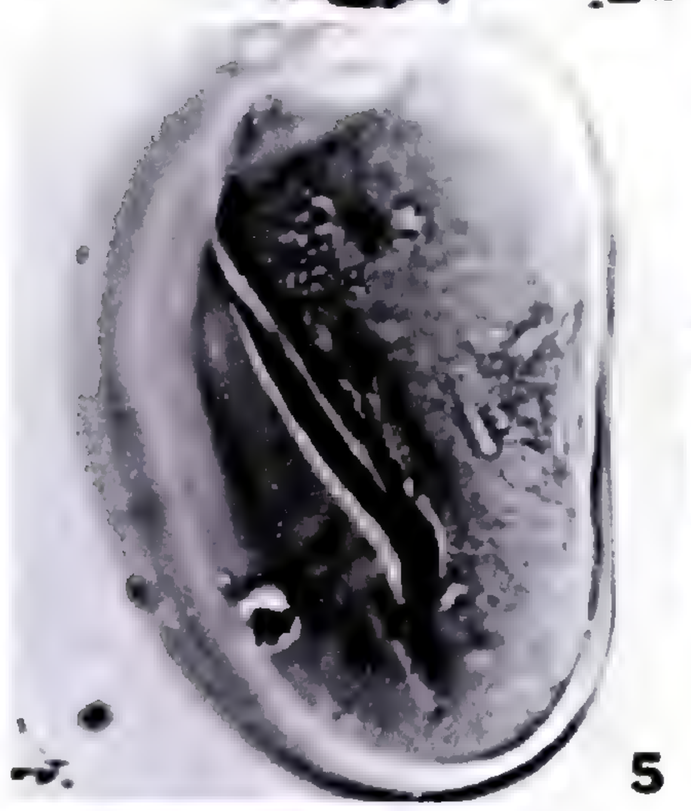

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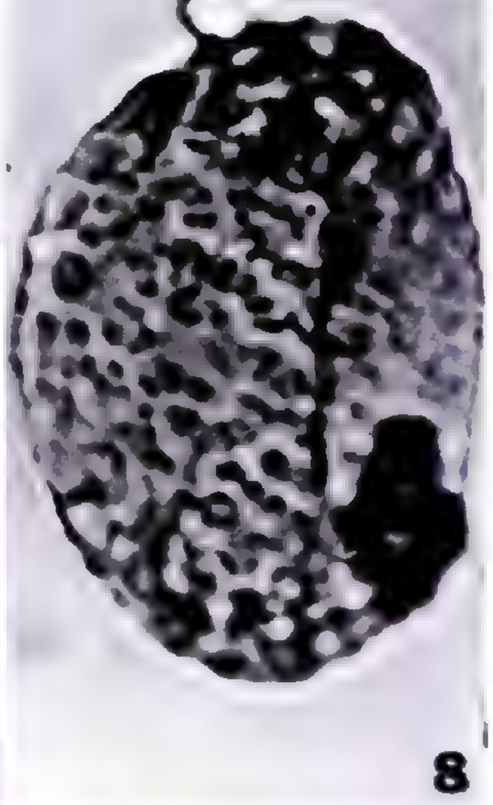
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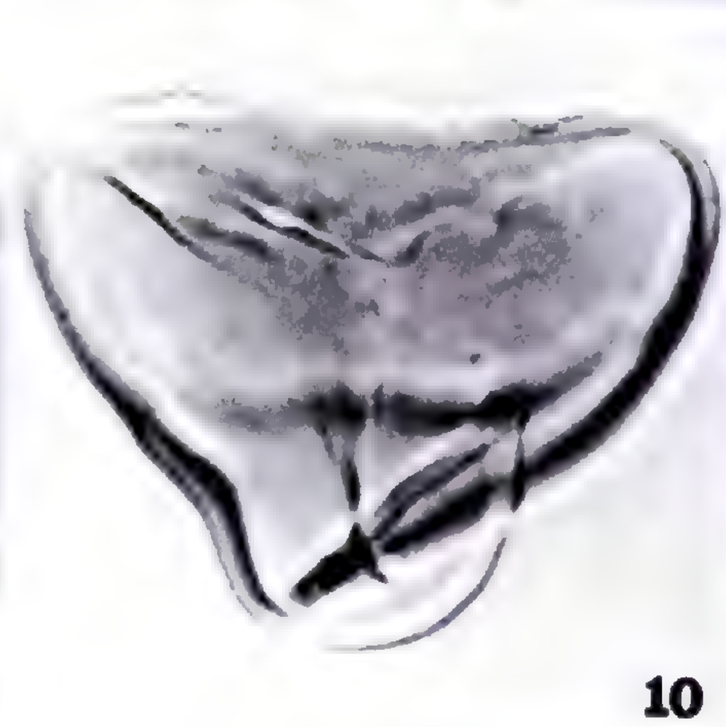
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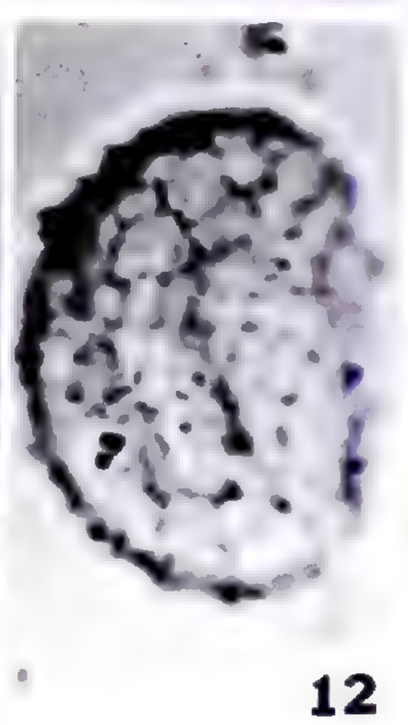
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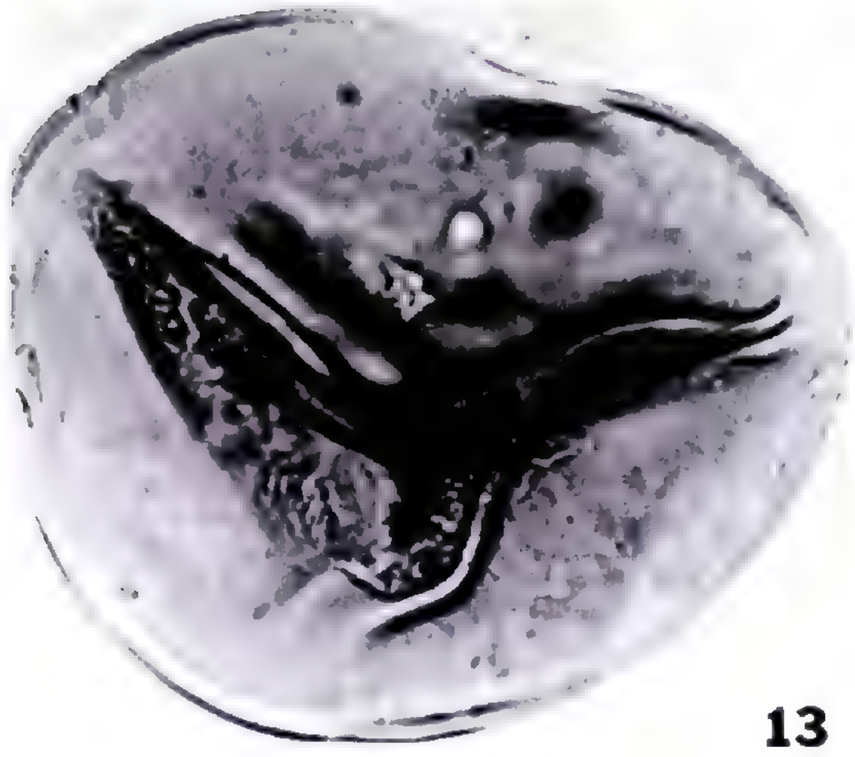
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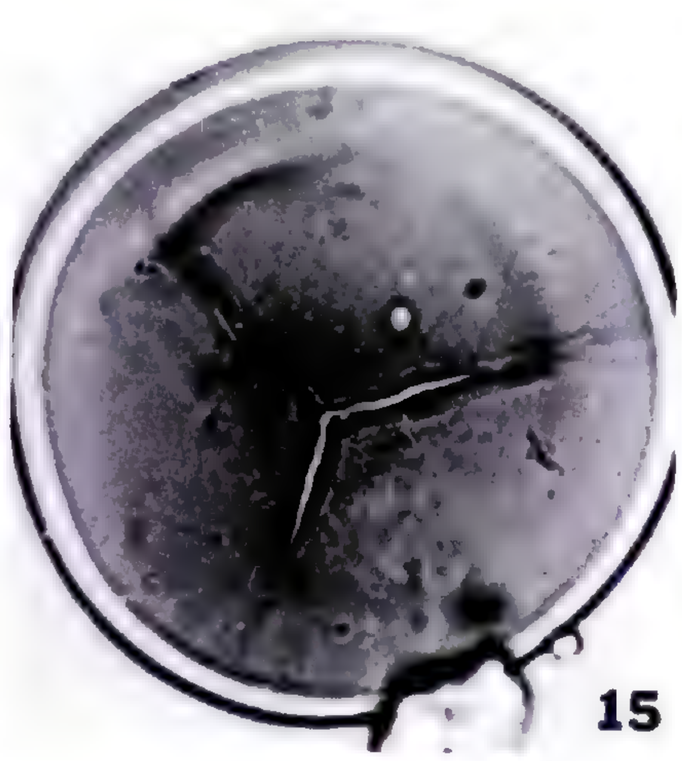
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punctate or microreticulate under electron microscope (EM) magnifications. In such instances the EM pattern can be given in parentheses; e.g., faintly scabrate (EM—microreticulate).

Results

SELAGINELLACEAE

Selaginella (Fig. 2a, b). Amb ca. circular; trilete, laesurae frequently obscured by wall thickness and sculpture elements, straight, narrow, inner margin entire, ca. 12–15 μm long, extending nearly to spore margin, tapering to acute apex; echinate, echinae short (ca. 2–3 μm), occasionally curved, base broad, distal face appearing irregularly reticulate due to arrangement of spine bases, proximal face less sculptured; wall 2–3 μm thick (excluding echinae); 25–30 μm and 40–50 μm.

Two size groups of *Selaginella* microspores are present, 25–30 μm (Fig. 2b) and 40–50 μm (Fig. 2a). Both are moderately frequent in samples 2 and 9 (Table 1) and occur scattered throughout the other samples. The genus has previously been reported from Caribbean deposits in the Oligocene of Puerto Rico (Graham & Jarzen, 1969) and in the Miocene of Veracruz, Mexico (Graham, 1976). *Selaginella* is presently distributed widely in tropical regions and is particularly abundant in shaded humid habitats.

PARKIACEAE

Ceratopteris (Fig. 3). Amb oval-triangular, spore margin undulating due to projecting sculpture elements; trilete, laesurae straight, narrow, inner margin entire, 25–30 μm long, extending ⅔ distance to spore margin, bordered by narrow (2 μm) ridged lip, lip surface psilate, margin entire; wall coarsely and conspicuously striate, striae psilate, margin slightly undulating, 2–3 μm wide, prominently developed on distal surface, less distinct approaching laesurae; wall 2–3 μm thick; 55–80 μm.

The genus *Ceratopteris* is a floating aquatic fern distributed from Florida through the Antilles and Central America into northern South America. The spores are common in the fossil record under the form-genus name *Cicatricosisporites*. Germeraad et al. (1968) described similar spores as *Magnastriatites*, but Dueñas (1980) considered these congeneric with *Cicatricosisporites*. In the Gatuncillo samples the spores are common in sample 9.

POLYPODIACEAE

Pteris (Fig. 4). Amb triangular, margin entire; trilete, laesurae straight, narrow, inner margin entire, ca. 20 μm long, extending nearly to spore margin; wall with coarse, irregular verrucae on distal surface, proximal surface more laevigate, marginal flange ca. hyaline, 4–5 μm wide; 45–50 μm.

The genus *Pteris* includes about 250 species widely distributed in Latin America. Although some species can occupy dry habitats as primary invaders, most grow in moist areas (in Panama, tropical moist forest; Croat, 1978).

TRILETE FERN SPORES (FIGS. 9, 10, 13–16)

In addition to *Ceratopteris* and *Pteris*, five other trilete spore types are represented in the Gatuncillo Formation. Although affinities may be suggested for some of these spores, their morphology is too general for definite generic identification.

Type 1 (Fig. 10). Amb triangular; trilete, laesurae slightly undulating, narrow, inner margin entire, 20–25 μm long, extending nearly to spore margin; wall 2 μm thick, laevigate; 35–40 μm.

This spore is similar to several species of *Adiantum*, but lacks diagnostic features separating it consistently from others (e.g., variants in spores of some species of *Dennstaedtia*). It is most common in sample 2 (2%).

Type 2 (Fig. 9). This spore differs from Type 1 in that the wall thickens at the apices and the ends of the laesurae are branched. 45 μm.

Type 3 (Fig. 13). The distinctive feature of this spore is its large size (120 μm), nearly double

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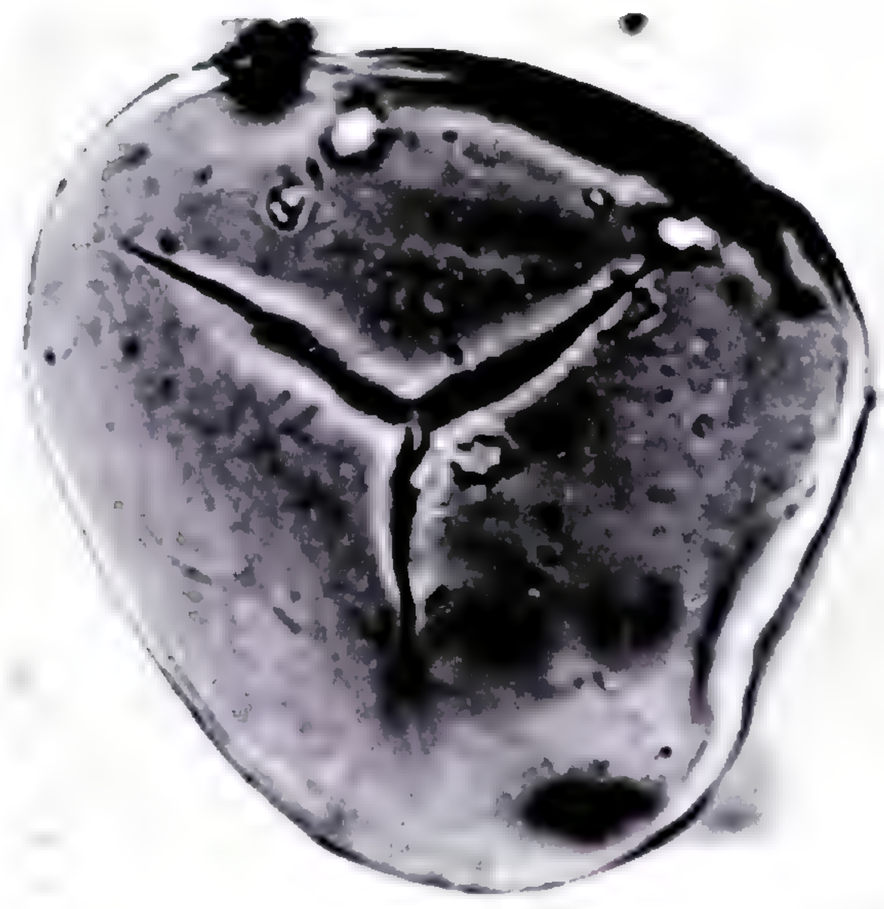
FIGURES 2–15. 2a. *Selaginella*, 2-1, V-27,1-3.—2b. *Selaginella*, 2-1, Q-31,2.—3. *Ceratopteris*, 9-1, S-36.—4. *Pteris*, 2-1, Q-39.—5. Monolete fern spore type 1, 4-1, O-22,2.—6. Monolete fern spore type 2, 2-1, G-39,2.—7. Monolete fern spore type 3, 4-1, T-7.—8. Monolete fern spore type 4, 2-1, T-32,1-3.—9. Trilete fern spore type 2, 4-1, R-10,4.—10. Trilete fern spore type 1, 4-1, X-8.—11, 12. Monolete fern spore type 5, 4-1, W-12,4.—13. Trilete fern spore type 3, 4-1, N-26,3-4.–14, 15. Trilete fern spore type 4, 4-1, M-38,1-2. (Numbers following plant names indicate the sample and slide number, and England Slide Finder coordinates. All material is labeled locality Pan D, = Gatuncillo Formation from the site described in the text.)



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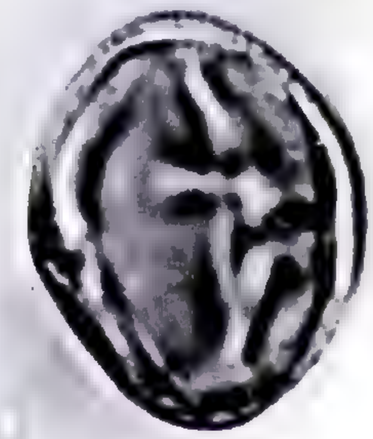

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that of the similar Type 5 (55–65 μm; Fig. 16). It is most common in sample 2 (2.5%).

Type 4 (Figs. 14, 15). Amb circular; trilete, laesurae straight, narrow, 27–30 μm long, extending ½–⅔ distance to spore margin, bordered by narrow, ridged lip; wall hyaline, 3–4 μm thick, laevigate, minute pits surrounding laesurae, concentrated in central contact region; 90–100 μm.

Type 5 (Fig. 16). This spore is similar to Type 3 except it is about half the size (55–65 μm). Similar spores are known in older sediments as *Deltoidospora* and have been reported recently from the Eocene of the Burgos Basin (northeastern Mexico; Martinez-Hernandez et al., 1980). Among spores in our reference collection it is similar to *Antrophytum* (Polypodiaceae). It is common in samples 2 (4%) and 4 (1.5%).

MONOLETE FERN SPORES (FIGS. 5–8, 11, 12)

Monolete fern spores usually cannot be identified to genus within the Polypodiaceae/Blechnaceae complexes. This is especially true of fossil spores that lack the enclosing perine. In the Gatuncillo material, two distinct monolete fern spores are common, and three others are present that may represent only variants or preservation forms.

Type 1 (Fig. 5). Amb reniform, outer margin entire; monolete, laesura along concave side, straight, narrow, 20–25 μm long, extending ca. ⅓ spore length; wall 2 μm thick, laevigate; 70–75 μm by 45–50 μm.

This spore belongs to the form-genus *Laevigatosporites,* which is a highly artificial taxon and, consequently, has an extensive stratigraphic range (Paleozoic to Recent).

Type 2 (Fig. 6). Amb reniform, outer margin lobate reflecting sculpture elements; laesura straight, narrow, inner margin entire, 30–35 μm long, extending ⅔ spore length; wall 3–4 μm thick, verrucate, verrucae prominent on distal surface, diminishing about laesura; 55–65 μm by 35–45 μm.

This spore type belongs to the form-genus *Verrucatosporites* which ranges from the Paleozoic to Recent.

Type 3 (Fig. 7). This spore is similar to Type 1 but has minute punctations over the entire surface. 45 μm by 35 μm.

Type 4 (Fig. 8). This spore is coarsely and irregularly punctate (corrosion artifact?). 50 μm by 35 μm.

Type 5 (Figs. 11, 12). This spore has echinae-like structures with the bases arranged to give a reticulate appearance. It is possible that this apparent sculpture represents remnants of a perine apressed to the spore surface. 50 μm by 35 μm.

BROMELIACEAE (FIGS. 17–21)

cf. *Tillandsia* Type 1 (Figs. 17–19). Prolate; monocolpate, colpus straight, narrow, inner margin entire, 45 μm long, extending nearly entire length of grain; tectate-perforate, wall thin (ca. 1.5–2 μm), reticulate, reticulum fine, lumen slightly irregular in outline, ca. 1–1.5 μm on distal surface, diminishing toward colpus and especially toward poles, muri ca. 1–1.5 μm wide, smooth, margins entire; 50–55 μm by 25–30 μm.

cf. *Tillandsia* Type 2 (Figs. 20, 21). Pollen of *Tillandsia* Type 2 differs from the preceding in having a much coarser reticulum. The diameter of the largest lumen is 3–4 μm (versus 1.5–2 μm). In other features the grains are similar.

The assignment of these grains to the Bromeliaceae is based on similarity to several species of *Tillandsia.* The specimen illustrated in Figure 19, for example, is especially similar to some grains of *T. excelsa* Griesb. (*Ocampo 001159,* Costa Rica, CR). Other fossil specimens are comparable in morphology but differ slightly in minor, quantitative features (e.g., almost immeasurable, minute differences in diameter of the lumen, wall thickness, height and/or width of the columellae, etc.). These differences are difficult to record accurately and consistently, but they do impart a different aspect to the grains that can be discerned visually. Consequently, the specimens are assigned to the next higher taxonomic rank (family Bromeliaceae), then compared (cf.) to the genus *Tillandsia.*

The fossil record suggests that the middle and

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FIGURES 16–31. 16. Trilete fern spore type 5, 2-1, J-24,4.—17, 18. cf. *Tillandsia* type 1, 4-1, W-30,2-4.—19. cf. *Tillandsia* type 1, 2-1, T-28.—20, 21. cf. *Tillandsia* type 2, 4-1, M-30,2-4.—22. Palmae type 3, 4-1, H-28,4.—23. Palmae type 1, 2-1, V-19,1-2.—24, 25. Palmae type 2, 4-1, V-20,4.—26. Palmae type 4, 2-1, D-16,2.—27. Palmae type 5, 2-1, L-22,1-3.—28, 29. cf. *Campnosperma,* 4-1, Q-25,3.—30, 31. cf. Araliaceae, 4-1, S-14.

late Eocene includes the time interval during which many angiosperms were differentiating into modern genera. In slightly older deposits (e.g., Paleocene, early Eocene) many, perhaps most, angiosperm pollen types cannot be assigned to modern genera. In slightly younger deposits (e.g., Oligocene) most do resemble modern genera. The upper Eocene is intermediate and the Gatuncillo Formation is part of this transition period.

The concepts and procedures illustrated by the identification of the Bromeliaceae cf. *Tillandsia* specimens are considered a conservative approach that minimizes misidentifications while providing the maximum taxonomic and biogeographic information that can reliably be derived from this difficult tropical Eocene material.

PALMAE (FIGS. 22–27)

Five morphological categories of palm pollen were recovered from the Gatuncillo Formation. The moderate diversity and sustained numerical representation suggest that palms were a significant, but not a dominant, element in the upper Eocene landscape of Panama (7.5% in sample 2; 6% in sample 4; 4.5% in sample 9; Table 1).

Type 1 (Fig. 23). Oblate, amb triangular to slightly oval triangular with rounded apices; trichotomocolpate, arms straight to slightly sinuous, 18 μm long, narrow, tapering to acute apex, inner margin entire to faintly dentate, extending within ca. 2–4 μm of outer margin; tectate, wall 1.5–2 μm thick, slightly thicker at apices; microechinate, echinae minute, blunt to pointed, densely aggregated, spaces between echinae giving microreticulate aspect to some areas of grain surface; 38–42 μm.

Pollen of the extant genus *Acrocomia* is similar to the microfossils in being trichotomocolpate but differs in details of sculpture pattern and wall thickness.

Type 2 (Figs. 24, 25). Reniform; monosulcate, sulcus straight to slightly sinuous, 24 μm long, inner margin faintly dentate, extending entire length of grain; tectate to tectate-perforate, wall ca. 1.5 μm thick; microreticulate (diam. of lumen less than 1 μm); 28–30 μm by 22–24 μm.

Species within a number of extant genera have pollen similar to the microfossils, including *Aiphanes, Chamaedorea* (e.g., *C. caspariana* Klotzsch), *Coccothrinax* [e.g., *C. argentea* (Lodd.) Sang.], and *Copernica.*

Type 3 (Fig. 22). Amb ca. wedge-shaped (widest part of grain above equator); monosulcate, sulcus sinuous, 52 μm long, inner margin entire, extending entire length of grain; tectate to tectate-perforate, wall ca. 1.5 μm thick; finely reticulate, muri smooth, inner margin entire, diam. of lumen ca. equal to width of muri (ca. 1 μm or less); 56–60 μm by 24–28 μm.

Type 4 (Fig. 26). Amb oval (elongated); monosulcate, sulcus straight, 36 μm long, inner margin minutely dentate, extending entire length of grain; tectate, wall ca. 1.5 μm thick; microreticulate (diam. of lumen less than 1 μm); 39–43 μm by 25–29 μm.

This grain is similar in aperture and sculpture pattern to Type 3, but the widest part of the grain is around the equator and it is considerably smaller.

Type 5 (Fig. 27). Amb ca. wedge-shaped (widest part above equator); monosulcate, sulcus straight, 32 μm long, inner margin dentate, extending entire length of grain; tectate-perforate, wall 2 μm thick; finely reticulate, muri smooth, inner margin entire, lumen ca. 1 μm; 37–41 μm by 20–24 μm.

ANACARDIACEAE

cf. *Campnosperma* (Figs. 28, 29). Prolate, amb oval; tricolporate, colpi straight, 18 μm long (apex to equator), narrow, tapering gradually to acute apex, inner margin entire, equatorially arranged, meridionally elongated, equidistant, costae colpi, pores equatorially elongated, 1 μm by 3 μm, situated at midpoint of colpus, inner margin entire; tectate-perforate, wall 1.5 μm thick; finely striato-reticulate; 24–26 μm by 19–21 μm.

The grains are similar to pollen of *Campnosperma* and, to some extent, *Comocladia. Campnosperma* consists of two species with one (*C. panamensis* Standley) native to Panama. They are most abundant in the West Indies and com-

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FIGURES 32–53. 32, 33. *Ilex,* equatorial view, 4-1, M-31.—34. *Ilex,* polar view, 9-1, G-23,3.—35. cf. *Paragonia/Arrabidaea,* 4-1, L-7,2.—36, 37. *Combretum/Terminalia,* equatorial view, 4-1, Q-25,4.—38, 39. *Combretum/Terminalia,* polar view, 4-1, U-38,1-2.—40, 41. cf. *Tetragastris,* 4-1, X-8,2.—42–44. cf. *Protium,* 9-1, D-22,1.—45, 46. *Casearia,* 4-1, K-35,2; 4-1, D-21,1.—47, 48, 52, 53. *Lisianthius,* 4-1, X-23; 4-1, V-34,1.—49, 50. cf. *Tontalea,* 9-1, M-38.—51. *Alfaroa/Engelhardia,* 4-1, C-35,1-2.

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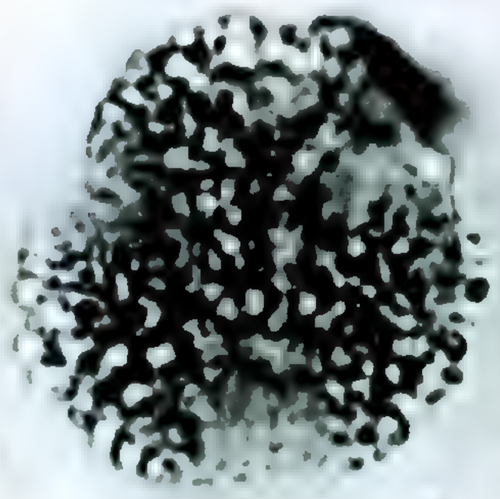
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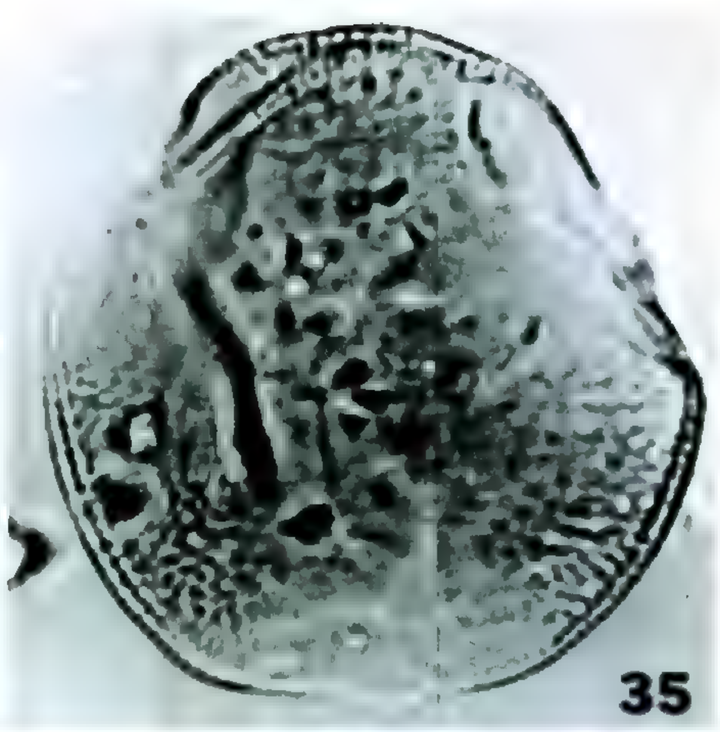
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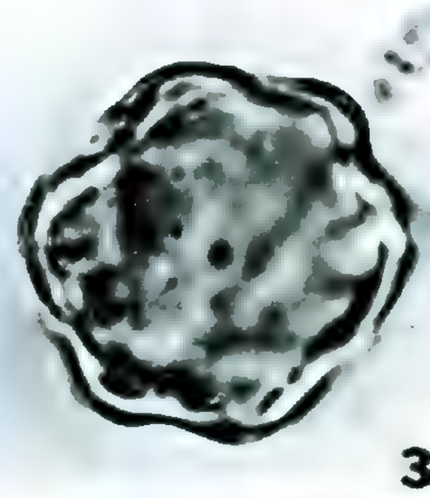
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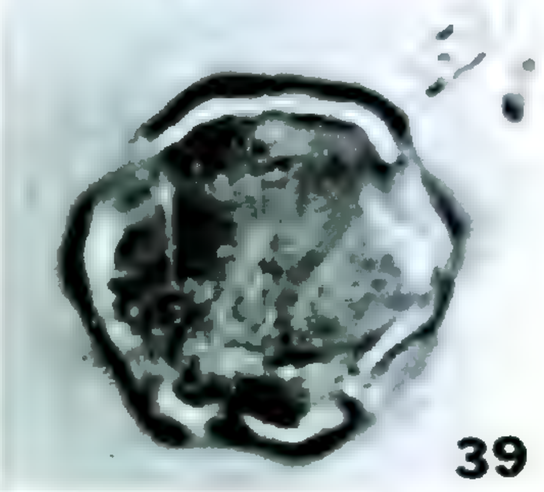
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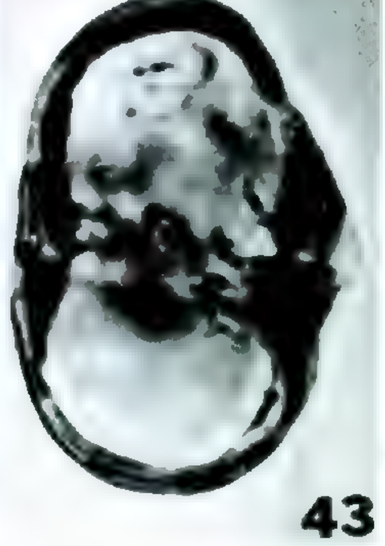
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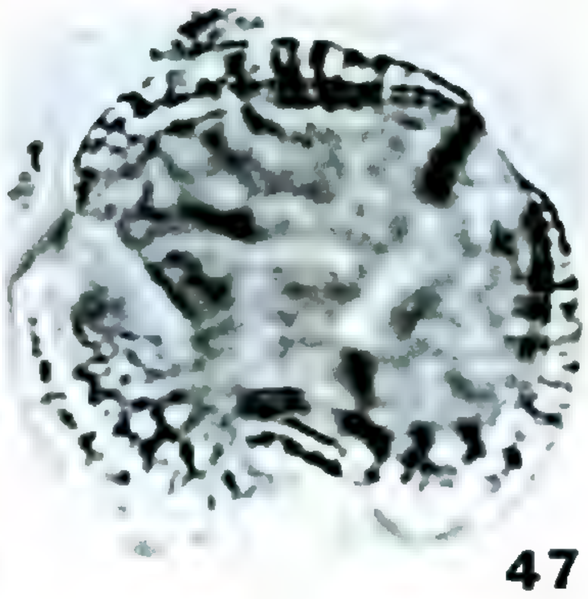
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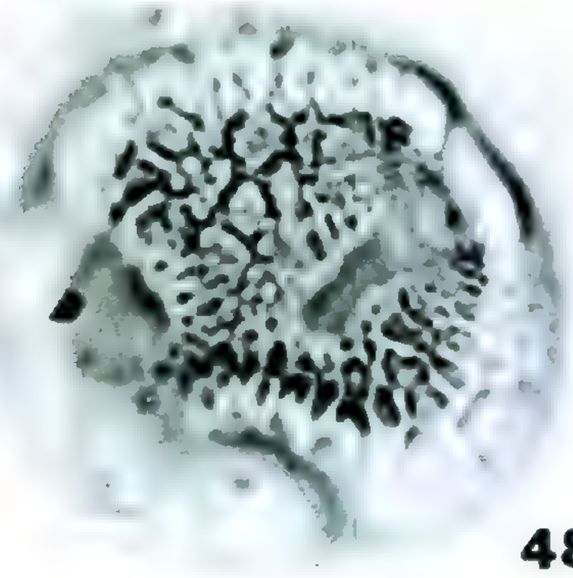
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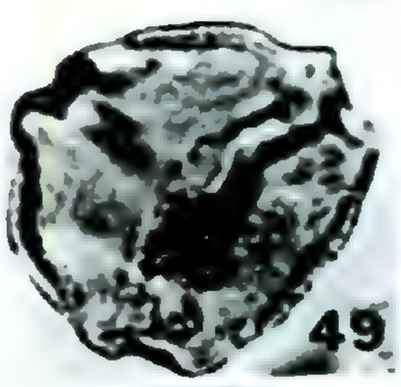
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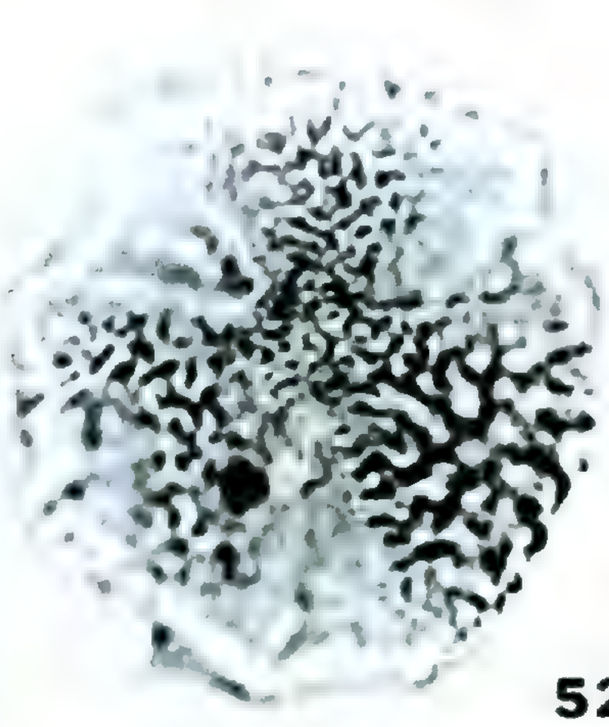
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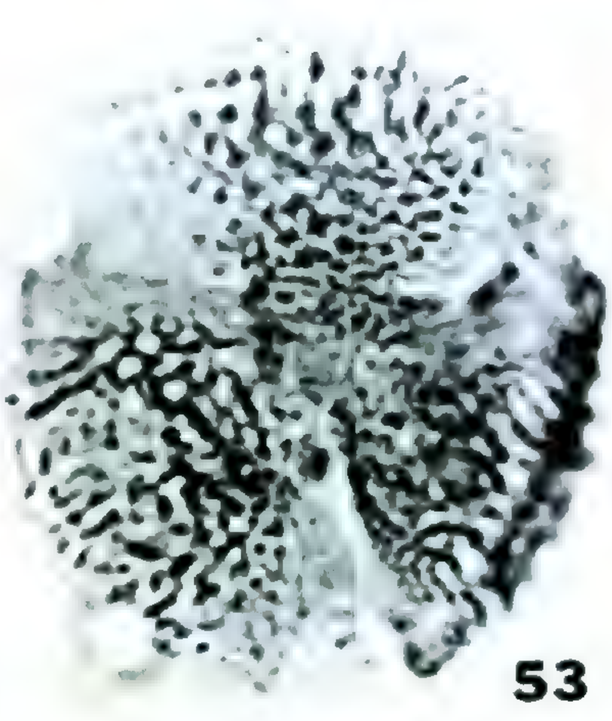
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monly grow in lowland, wet habitats such as swamps.

AQUIFOLIACEAE

Ilex (Figs. 32–34). Oblate-spheroidal, amb circular; tricolporoidate, colpi straight, 10 μm long, broad (ca. 9 μm at midpoint), inner margin diffuse, tapering to acute apex, equatorially arranged, meridionally elongated, equidistant, extending within 6 μm of pole (P.I. 0.27), pores obscure, diam. ca. 2–3 μm, ca. circular, situated at midpoint of colpus; intectate, wall thickness (viz., height of columellae) 3 μm; clavate; 25–32 μm.

Ilex is a widespread genus of about 400 species. In Latin America it commonly occurs in mesic to slightly drier habitats. For example, in the Antilles it grows in the high-altitude pine forests (Howard, 1973); in Veracruz it is a member of the low evergreen selva, the high semi-evergreen selva, and the bosque caducifolio (Gomez-Pompa, 1973); and in Panama it is found at mid-altitudes in drier forest habitats and late secondary forests (Porter, 1973).

Fossil pollen of *Ilex* appears in the early Late Cretaceous of Australia, late Late Cretaceous of North America, and Paleocene of South America (Muller, 1981). By Tertiary times it is virtually cosmopolitan. In northern Latin America *Ilex* is known from the Eocene of Panama (this report), the Oligocene of Puerto Rico (Graham & Jarzen, 1969), the Miocene of Veracruz, Mexico (Graham, 1976), the Miocene of Panama (Graham, 1985), and the Quaternary of Panama (Bartlett & Barghoorn, 1973).

CF. ARALIACEAE (FIGS. 30, 31)

Prolate to prolate-spheroidal, amb circular; tricolporate, colpi straight, 10 μm long, inner margin entire, tapering to acute apex, equatorially arranged, meridionally elongated, equidistant, pore obscure, slightly elongated equatorially, ca. 1–1.5 μm by 2.5 μm, situated at midpoint of colpus; tectate-perforate, wall 1.5–2 μm thick; finely reticulate; 21–24 μm.

The primary purpose of including this microfossil is to document the occurrence of Araliaceae-type pollen in the assemblage, even though the specimens cannot be identified to genus.

BIGNONIACEAE

cf. *Paragonia/Arrabidaea* (Fig. 35). Oblate, amb circular; tricolporate, colpi straight, 18 μm long, broad (ca. 10 μm at equator), equatorially arranged, meridionally elongated, equidistant, tapering to acute apex, margin diffuse; tectate to tectate-perforate, wall ca. 1.5 μm thick; finely reticulate; 45 μm.

Modern pollen of the Bignoniaceae has been studied by Gentry and Tomb (1979). Based on their survey, and material in our reference collection, the microfossil is most similar to *Paragonia* [*P. pyramidata* (Rich.) Bur.] and to *Arrabidaea* [e.g., *A. corallina* (Jacq.) Sandw.]. One collection of *Paragonia* (*Croat 7895,* BCI, Panama, MO) is especially similar in being relatively large, thin-walled, and having a diffuse colpus margin. Pollen from two other collections (Harvard exchange) differ in being smaller, thick-walled, and with distinct costae colpi.

Arrabidaea and *Paragonia* are both lianas distributed from Mexico to Brazil, Bolivia, and the former to Argentina. *Paragonia* is widespread in the tropical moist and wet forests of Panama. Both *Arrabidaea* and *Paragonia* produce numerous flowers in terminal panicles and are among the most common bignoniaceous vines in Panama. *Paragonia* "flowers in extravagant bursts lasting about a month, abundantly in the dry season and erratically throughout the year" (Croat, 1978: 768), and the various *Arrabidaea* species have similar flowering peaks spaced throughout the year (Gentry, 1974). These features are consistent with small percentages in the fossil record (1% or less, Table 1) even though the genera are insect-pollinated lianas of the forest canopy.

BURSERACEAE

The two principal neotropical genera of the Burseraceae are distinguished palynologically by the striato-reticulate pollen of *Bursera* (ca. 80 species) and the psilate pollen of *Protium* (ca. 90 species). Within the latter, however, there are other smaller genera with similar pollen (e.g., *Crepidospermum,* 2 species; *Hemicrepidospermum,* 1 species; *Tetragastris,* 8–12 species). Two subtypes of this prolate, psilate pollen are recognized in the Gatuncillo assemblage. One is comparatively thick-walled and is most similar to pollen of *Protium.* The other is thin-walled with a more hyaline appearance and is comparable to *Tetragastris.* Because there is some overlap in pollen morphology among these modern genera, however, the fossils are referred to cf. *Protium* and cf. *Tetragastris.*

cf. *Tetragastris* (Figs. 40, 41). Prolate; tri-

colporate, colpi narrow, straight, ca. 25 μm, inner margin entire, sides parallel, apex acute, equatorially arranged, meridionally elongated, equidistant, distinct costae colpi and costae pori 4 μm thick in equatorial region surrounding pore, pore elongated equatorially, 2.5 μm by 6 μm, situated at midpoint of colpus, inner margin entire; tectate, exine relatively thin (1.5 μm); psilate, hyaline; 32 μm by 24 μm.

Tetragastris is a tree or shrub distributed from Brazil northward through the Antilles (to Hispaniola) and Central America to British Honduras. The most common species is *T. panamensis* (Engl.) O. Kuntze found in British Honduras, Honduras, Nicaragua, Costa Rica, Panama, Venezuela, the Guianas, Brazil, and Peru. It is widespread in Panama and Porter (1970), citing Johnston (1949), noted that it is "an important forest tree on San Jose Island, where it may make up more than half of the canopy layer . . . ." According to Croat (1978), the species is ecologically variable and ranges from tropical moist to tropical dry forests. There are no other reports of *Tetragastris* in the fossil record.

cf. *Protium* (Figs. 42–44). Prolate; tricolporate, colpi narrow, faint, straight, ca. 26 μm, inner margin entire, sides parallel, apices acute, equatorially arranged, meridionally elongated, equidistant, costae colpi and costae pori 3.5 μm thick in equatorial region surrounding pore, pore equatorially elongated (colpi transversalis), 2.5 μm by 8 μm, situated at midpoint of colpus, inner margin entire; tectate, wall 2.5 μm thick; psilate; 36 μm by 24 μm.

Protium is a tree or shrub of the tropical forests of both the New and Old Worlds. In the neotropics it is most common in South America, with seven species listed for Panama (Porter, 1970). Throughout Central America it occurs in the tropical moist, premontane wet, and tropical wet forests. The fossil record of the Burseraceae is poorly known, with tentative reports that may extend the range of the family back to the lower Eocene (Muller, 1981). In the Caribbean area, *Protium*-type pollen is recorded from the upper Miocene Paraje Solo Formation of Veracruz, Mexico (Graham, 1976).

COMBRETACEAE

Combretum/Terminalia (Figs. 36–39). Prolate to prolate-spheroidal, amb circular (lobate reflecting arrangement of apertures); tricolporate with 3 pseudocolpi, colpi straight, ca. 22–25 μm, inner margin entire, narrow, sides parallel for most of length, then tapering near terminus to acute apex, equatorially arranged, meridionally elongated, equidistant, extending within 5 μm of pole (P.I. 0.2), pore (endoaperture) frequently obscure, circular, diam. ca. 3 μm, situated at midpoint of colpus; tectate, wall 1.5 μm thick; psilate to faintly scabrate; 25–30 μm by 18–22 μm.

The microfossils oriented in polar view (Figs. 38, 39) are most similar to *Combretum/Terminalia* pollen because the pore is more evident. Some microfossils oriented in equatorial view (Figs. 36, 37) are comparable in size, shape, sculpture, structure, and in the presence of multiple apertures (colpi), but the pore is obscure. In the pollen of most modern species of *Combretum/Terminalia* the pore is visible in equatorial view, but occasionally it is less obvious. The grain illustrated in Figures 38 and 39 is typical of *Combretum/Terminalia,* while those represented by Figures 36 and 37 are regarded as likely belonging to the same complex.

It is not possible to consistently distinguish *Combretum* and *Terminalia* pollen under light microscopy when they are encountered as isolated microfossils (Graham, 1980); hence, the designation *Combretum/Terminalia.* Similar pollen occurs in the Melastomataceae, but it is either smaller (9–15 μm) and/or has distinct costae colpi.

Both *Combretum* and *Terminalia* are widespread in Latin America and most commonly occur in wet to moist forests, although *C. fruticosum* (Loeff.) Stunz can range into drier habitats. The microfossils are also known from the Miocene of Veracruz, Mexico (Graham, 1976) and from the Quaternary of Panama (as *Combretum*; Bartlett & Barghoorn, 1973). Muller (1981) cited other occurrences that extend the complex into the upper Eocene of Cameroon, and it is now known also from the upper Eocene of Panama (this report). If this is the approximate complete stratigraphic range of *Combretum/Terminalia,* it may explain the difficulty in identifying certain types from the Gatuncillo assemblage, because the group would be in its early stage of differentiation.

FLACOURTIACEAE

Casearia (Figs. 45, 46). Prolate; tricolporate, colpi narrow, straight, 22–24 μm, inner margin faintly undulating, apices acute, equatorially arranged, meridionally elongated, equidistant, nar-

row costae colpi, pore equatorially elongated (colpi transversalis), 2 μm by 5 μm, situated at midpoint of colpus, inner margin entire; tectate, wall 1.5 μm thick; microreticulate; 30–35 μm by 22–25 μm.

Casearia includes about 250 species of trees and shrubs widely distributed in tropical to subtropical regions of both hemispheres. Eight species are listed for Panama (Robyns, 1968), and these generally occur in moist forest types, although some (e.g., *C. arguta* H.B.K., *C. commersoniana* Camb.) range into the drier premontane or tropical dry forests (Croat, 1978). Pollen morphology of the family has been studied by Keating (1973). The fossil pollen is most similar to *C. sylvestris* Sw. In the Caribbean region, *Casearia* has been reported from the Oligocene of Puerto Rico (Graham & Jarzen, 1969) and the upper Miocene of Veracruz, Mexico (Graham, 1976). The present report from the Gatuncillo Formation extends the fossil record to the upper Eocene.

GENTIANACEAE

Lisianthius (Figs. 47, 48, 52, 53). Oblate to oblate-spheroidal, amb circular; tricolporate, colpi broad at equator, tapering to acute apex, ca. 18 μm long (equator to apex), extending within 6–7 μm of pole (P.I. 0.02), equatorially arranged, meridionally elongated, equidistant, inner margin entire to slightly diffuse, faint margo formed by gradual diminution of reticulum near colpus margin, pore circular, 4–5 μm, situated at midpoint of colpus, margin diffuse; tectate-perforate, height of columellae 2.5 μm in equatorial mesocolpal region, diminishing toward poles and margins of colpi; reticulate, reticulum somewhat irregular, diam. of lumen ca. 2–3 μm in equatorial mesocolpal region, diminishing toward poles and margins of colpi, muri tall (ca. 2.5 μm) in equatorial mesocolpal area, giving boxwork effect to reticulum, muri surface psilate, margins entire; 35–45 μm.

The presence of *Lisianthius* pollen in the Gatuncillo Formation has been reported earlier (Graham, 1984). The plants grow from south-central Mexico, through the Antilles and Central America, into northwest Colombia (Weaver, 1972; Elias & Robyns, 1975). They are found in a variety of habitats including secondary scrub, pine forests, cloud forests, and savannahs ranging from sea level to about 1,800 m. Of particular interest from the standpoint of the fossil pollen record is that, although primarily insect-pollinated, many species are highly floriferous and occur in dense stands at moderately low elevations. Fossils of the Gentianaceae are known from the lower Eocene of Texas, and other records extend its range into the Paleocene (Crepet & Daghlian, 1981). The Gatuncillo material represents the first report of *Lisianthius* in the fossil record.

HIPPOCRATIACEAE

cf. *Tontalea* (Figs. 49, 50). Oblate, amb ca. circular, undulating; tricolporate, colpi narrow, straight, 12 μm long, inner margin minutely dentate, apices acute, extending within 3–4 μm of pole (P.I. 0.015), equatorially arranged, meridionally elongated, equidistant, narrow margo, pore circular, 3 μm, situated at midpoint of colpus; tectate to tectate-perforate, ektexine thicker (columellae longer) in equatorial mesocolpal area (ca. 2 μm), thinning toward apertures (1.5 μm); finely reticulate; 26 μm.

Tontalea is a neotropical genus consisting of about 31 species of lianas, slender shrubs, or small trees. Only one [*T. richardii* (Pery.) A. C. Smith] occurs in Panama (Dodson & Robyns, 1965). This species is a liana common in the upper canopy of the tropical moist forest, although it is occasionally found at lower elevations and along the coast (Croat, 1978). Two other genera in the family contain species with pollen generally similar to *Tontalea* (*Cueruea, Pristimera*), but in the fineness of the reticulum and in wall structure (columellae) as seen in optical section, the fossil pollen is most similar to *Tontalea*. The genus has not previously been reported in the fossil record.

JUGLANDACEAE

Alfaroa/Engelhardia (Fig. 51). Oblate, amb oval-triangular; triporate, pore circular, ca. 2 μm, inner margin entire, equatorially arranged, equi-

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FIGURES 54–71. 54. *Crudia,* 2-1, T-21,1-3.—55, 56. Malpighiaceae type 1, 4-1, C-22.—57. Malpighiaceae type 2, 9-1, H-45,3.—58. cf. *Ficus,* 4-1, W-12,1-2.—59. *Eugenia/Myrcia,* 2-1, E-30,3.—60. *Eugenia/Myrcia* tetra-aperturate form, 4-1, V-24.—61. *Rhizophora,* 4-1, K-24,1.—62, 63. *Coccoloba,* 4-1, X-7,2-4.—64, 65. *Faramea,* 2-1, G-14,2; 9-1, K-39,4.—66, 67. Rubiaceae type 1, 4-1, G-17,1-3.—68, 69. Rubiaceae type 2, 4-1, S-14.—70, 71. *Paullinia,* 4-1, V-11,1-2.

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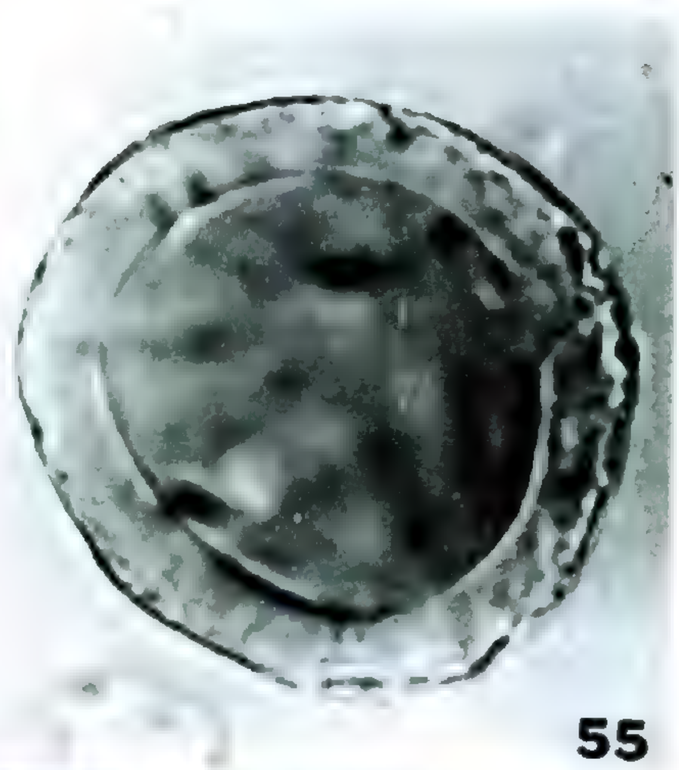
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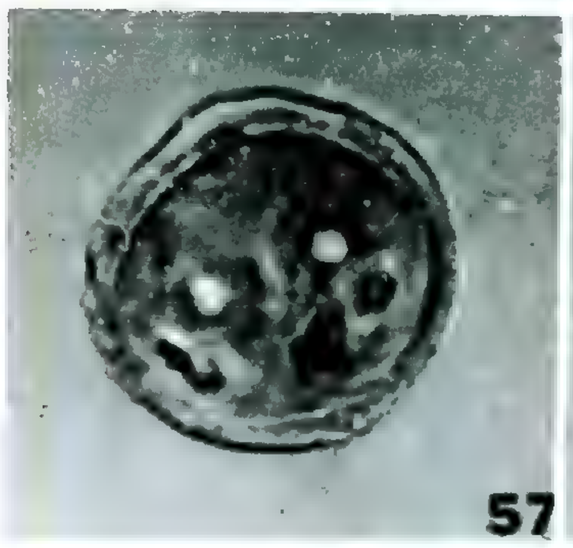
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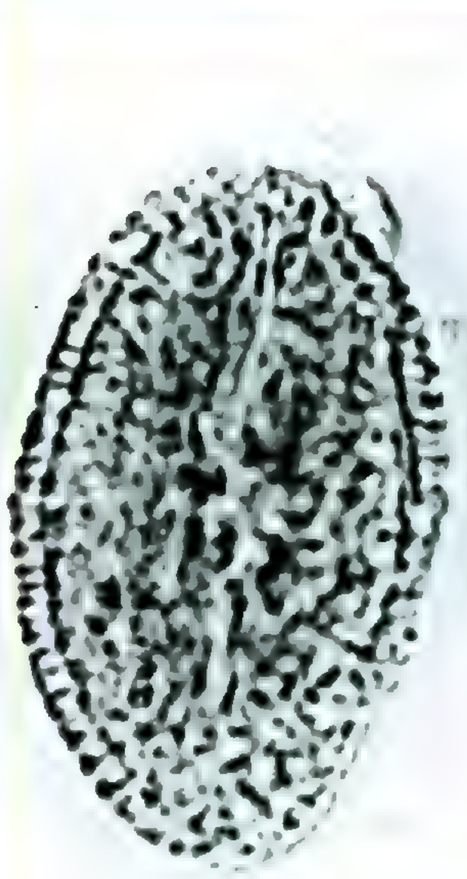
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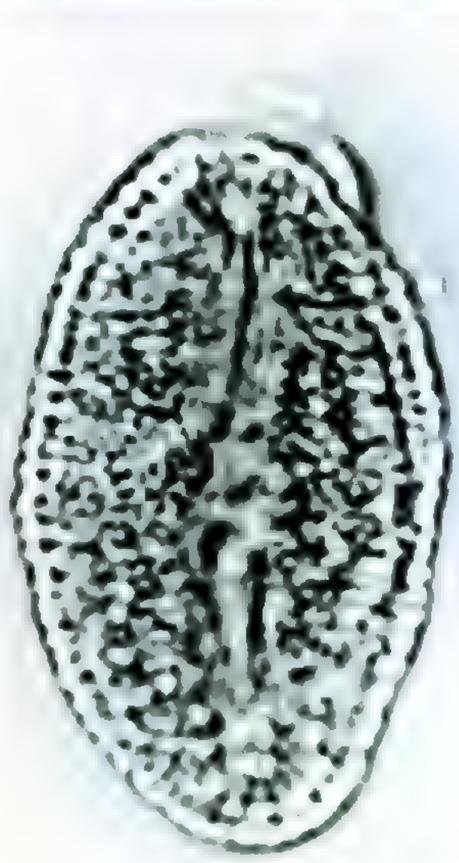
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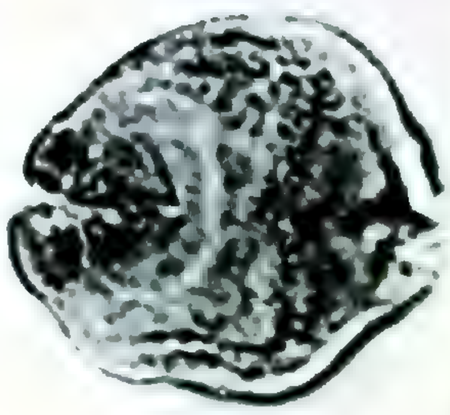
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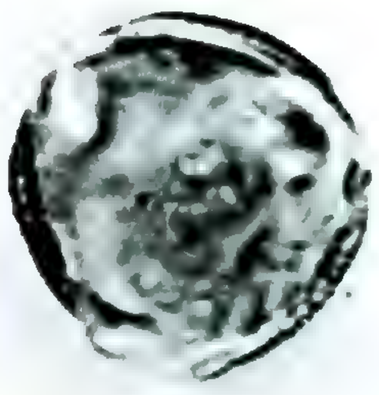
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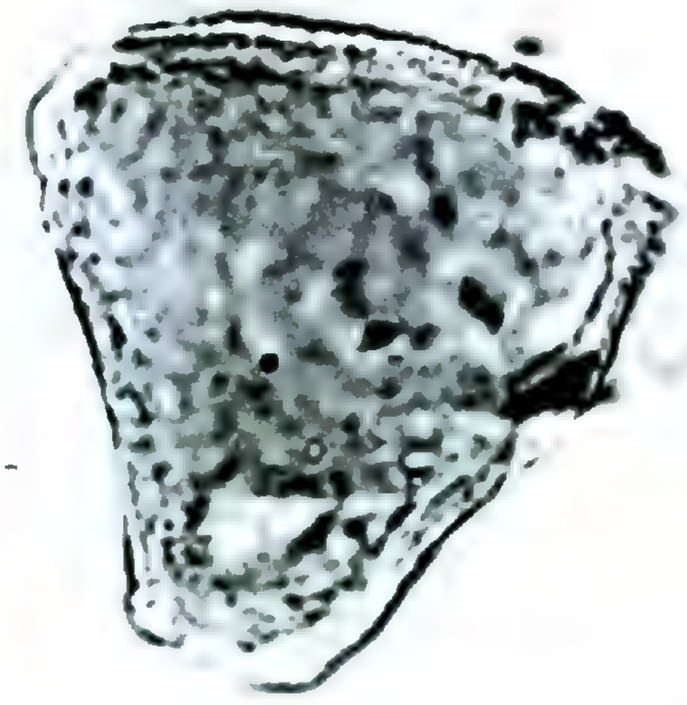
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distant; tectate, wall 1.5 μm thick; psilate to faintly scabrate; 26 μm.

Whitehead (1965) and Nichols (1973) conclude that *Engelhardia* and *Alfaroa* cannot consistently be distinguished on the basis of pollen morphology. Crepet et al. (1980) noted that one exception may be the distinctly smaller and triangular pollen of section *Psilocarpeae* of *Engelhardia*. Since our Gatuncillo material is not of this type, it is referred to *Alfaroa/Engelhardia*. Similar pollen is stratigraphically and geographically widespread throughout the Caribbean Tertiary and is a common microfossil in temperate regions of the northern hemisphere (Muller, 1981; Crepet et al., 1980). The fossil pollen is frequently referred to the form-genus *Momipites*. It is known from the Oligocene San Sebastian Formation of Puerto Rico (Graham & Jarzen, 1969), the Oligo-Miocene of Chiapas, Mexico (Langenheim et al., 1967), and the upper Miocene Paraje Solo Formation of Veracruz, Mexico (Graham, 1976). In the Gatuncillo material the pollen is rare (three grains encountered among the three samples studied). Both *Alfaroa* and *Engelhardia* occur in Central America (Manning, 1960) and are typically, but not exclusively, associated with temperate forests.

LEGUMINOSAE/CAESALPINIOIDEAE

Crudia (Fig. 54). Prolate; tricolporoidate; colpi narrow, straight, 22–38 μm, frequently obscured by sculpture elements, extending nearly entire length of grain, equatorially arranged, meridionally elongated, equidistant, pore area faint, ca. circular, situated at midpoint of colpus; tectate, but with occasional separations between sculpture elements, wall 1.5 μm thick; distinctly and coarsely striate, striae generally oriented parallel to long axis of grain, surface psilate, margins entire, occasionally appearing beaded from underlying pores in foot layer/endexine; 42 μm by 27 μm.

In the Caesalpinioideae 12 genera have striate pollen, but only two of these (*Crudia, Macrolobium*) are closely similar to the microfossils and occur in the New World. The genus *Macrolobium* has about 60 species that grow in tropical America. The pollen of these differ from the fossil in having more coarse, thick striations and/or with a much more conspicuous beaded appearance to the striations imparted by the underlying pores. The genus *Crudia* has about 55 species with ten growing in the neotropics. These are mainly Amazonian and often riverine species (Cowan & Polhill, 1981: 131; pollen morphology, Graham & Barker, 1981). *Crudia*-type pollen (under the form-genus name *Striatocolpites catatumbus* Gonzalez) is known back to the Eocene in northern South America and to the Paleocene in Nigeria (Muller, 1981).

MALPIGHIACEAE

Pollen of the Malpighiaceae is distinctive, but within the family generic identifications are difficult. Fossil pollen is common, but at low frequencies, in the Caribbean Tertiary. In the Gatuncillo Formation two pollen types belonging to the Malpighiaceae are present, but these cannot be referred to any one genus in the family.

Type 1 (Figs. 55, 56). Spherical, amb circular; pericolporate, colpi ca. straight to slightly sinuous, narrow, 22–24 μm, apices acute, inner margin minutely dentate, pores oval to slit-like, long axis at right angle to colpus, 1 μm by 3.5 μm, situated at midpoint of colpus, inner margin entire to minutely dentate; tectate, wall conspicuously thick (5 μm); minutely punctate-microreticulate; 44 μm.

Type 2 (Fig. 57). Spherical, amb circular; pericolporate, colpi straight, narrow, short (2–4 μm), faint, pores conspicuous, circular to oval, 2.5 μm, situated at midpoint of colpus, inner margin entire, distinct annulus ca. 2.5 μm wide; tectate, wall 3 μm thick; scabrate; 27 μm.

MORACEAE

cf. *Ficus* (Fig. 58). Prolate, amb oval; diporate, pores ca. circular, ca. 1.5 μm, situated at apices of grain; tectate, wall ca. 1.5 μm thick; scabrate; 10 μm by 13 μm.

In most diporate Moraceae pollen the pores are equatorial, frequently with an annulus, and are more spherical than the microfossil with a somewhat thicker wall. The fossil pollen is most similar to *Ficus*, but generic distinctions are so subtle that the microfossils are referred to cf. *Ficus*. The genus is large (ca. 1,000 species worldwide) and poorly understood taxonomically. In Panama, *Ficus* is most commonly associated with the moist forest type but can range into drier habitats. As expected from the pollination mechanism and floral structure, pollen of cf. *Ficus* is rare in the Gatuncillo palynoflora. In the stratigraphic literature the pollen type is known as *Psiladiporites minimus* van der Hammen & Wymstra and ranges from lower Miocene to Recent (Germeraad et al., 1968). The Gatuncillo

occurrence extends the range back to the upper Eocene.

MYRTACEAE

Eugenia/Myrcia (Figs. 59, 60). Oblate to peroblate, amb triangular; tricolporate, colpi narrow, straight, 10–12 μm, inner margin slightly dentate, equatorially arranged, meridionally elongated, equidistant, syncolpate, pores ca. 1 μm, situated on equator at midpoint of colpus; tectate, wall thin (ca. 1.5 μm), faintly scabrate; 17–19 μm.

Pollen of *Eugenia* and *Myrcia* is similar, and it is not possible to consistently refer isolated microfossils to either genus (Graham, 1980). This pollen type is common in Gulf/Caribbean Tertiary deposits, ranging from the middle Eocene (Elsik & Dilcher, 1974) to Recent. An occasional tetracolporate form is encountered (Fig. 60), and these are matched by modern species that include some multiaperturate pollen [e.g., *E. rhombea* (Berg.) Krug & Urb.]. The modern genera are important components of neotropical vegetation but collectively range through a wide variety of habitats which reduces their usefulness in paleoecological reconstructions.

POLYGONACEAE

Coccoloba (Figs. 62, 63). Prolate; tricolporate, colpi narrow, straight, extending nearly entire length of grain, 30–38 μm long, apices acute, inner margin entire, equatorially arranged, meridionally elongated, equidistant, costae colpi, pore (endoaperture) frequently obscure, ca. circular, 2–3 μm, situated at midpoint of colpus; tectate-perforate, wall thick (3 μm), columellae thick and clearly evident in optical section, sexine (tops of columellae) distinct from nexine (foot layer); reticulate, diam. of lumen ca. 1 μm; 39–50 μm by 23–36 μm.

Coccoloba is common in moist forest types of tropical America. Howard (1960) recognized 12 species for Panama, and several of these range into lowland coastal habitats where pollen can readily be incorporated into accumulating sediments. Microfossils are common in the Gatuncillo Formation (3.5% in sample 4; 2% in sample 9; Table 1), and in the upper Miocene Paraje Solo Formation of Veracruz, Mexico (Graham, 1976). The Eocene specimens from Panama cannot be related to a single modern species but are quite similar to *C. belizensis* Standley.

RHIZOPHORACEAE

Rhizophora (Fig. 61). Prolate to prolate-spheroidal; tricolporate, colpi narrow, straight, 14–16 μm, apices acute, equatorially arranged, meridionally elongated, equidistant, costae colpi ca. 3 μm, pores elongated equatorially (colpi transversalis), 1 μm by 4 μm, constricted at midpoint of colpus, inner margin entire; tectate-perforate, wall thick (2–3 μm); finely reticulate; 19–21 μm by 22–24 μm.

Fossil pollen of *Rhizophora,* also listed in the literature under the form-genus name *Zonocostites,* is almost by definition an important component of Tertiary lignites in warm-temperate to subtropical regions that form under coastal, brackish-water conditions (Cohen & Spackman, 1972; Scholl, 1964a, 1964b). Pollen of the six species (and one hybrid) are similar, but sufficient differences exist to tempt species distinctions in the fossil record. Modern and fossil pollen of *Rhizophora* was studied by Langenheim et al. (1967), Leopold (1969), and Muller and Caratini (1977). The last authors concluded that three groups of species can be recognized on the basis of pollen morphology: *R. mucronata/stylosa; R. apiculata/lamarckii/mangle;* and *R. racemosa.*

The microfossils in the upper Eocene Gatuncillo Formation are difficult to identify because they are near the apparent time of early diversification and radiation of the genus. The oldest known records are from the lower to middle Eocene of southeast Asia (Muller & Caratini, 1977), and the genus first appears in tropical America in the late Eocene (viz., Gatuncillo time). As a result, there are a number of microfossils in our Panama material that appear similar to *Rhizophora* but are quite small (14–16 μm by 18–20 μm) and sufficiently close to spherical as to orient in various views, precluding determining exact shape and/or aperture morphology. Many 'unknowns' in this category represent *Rhizophora*-like pollen and may be early forms of the pollen in these tropical American sediments. The specimen in Figure 61 is a more typical example of *Rhizophora* in the Gatuncillo Formation.

RUBIACEAE

Faramea (Figs. 64, 65). Oblate, amb oval; diporate, pores (short colpi) 6–7 μm (apex to equator), inner margin entire, apices ca. rounded, situated at poles (apices of long axes), broad diffuse costae pori (colpi) 4–5 μm wide, giving

stained effect to region surrounding aperture; tectate-perforate, wall ca. 1 μm thick; finely reticulate; 27–30 μm by 24–30 μm.

Faramea is a genus of about 125 species of trees and shrubs widely distributed in the Antilles, Central America, and South America (Dwyer, 1980). The pollen is typically triporate and reticulate, common to the family Rubiaceae, and these pollen types have been recorded from the Oligocene San Sebastian Formation of Puerto Rico (Graham & Jarzen, 1969) and the upper Miocene Paraje Solo Formation of Veracruz, Mexico (Graham, 1976). Among the species with normal triporate pollen, however, are some in our reference collection (e.g., *F. coarinensis* Muell. Arg.) in which many of the grains are diporate. The Gatuncillo specimens are all of the diporate type. Consequently, the known stratigraphic range of the genus is upper Eocene to Recent, but the diporate form is known only from the upper Eocene, and the triporate type ranges from the middle Oligocene to Recent. The present report extends the range back into the Eocene from that reported in Muller (1981).

Pollen of the Rubiaceae is abundant in the Gatuncillo Formation, but it frequently belongs to a generalized type common to many genera in the family. Two of the more common forms are described below.

Type 1 (Figs. 66, 67). Oblate to oblate-spheroidal, tricolporate, colpi short (6–8 μm), broad (ca. 4 μm at equator), tapering to ca. acute apex, inner margin entire, equatorially arranged, meridionally elongated, equidistant, pore elongated equatorially (colpi transversalis), 1 μm by 4 μm, situated at midpoint of colpus; tectate-perforate, wall ca. 1 μm, slightly thicker in mesocolpal region; finely reticulate; 18–23 μm.

This pollen type is common to several genera of the Rubiaceae, including especially *Antirrhoea,* but also *Calycophyllum, Erithalis,* and others.

Type 2 (Figs. 68, 69). This rubiaceous grain is similar to Type 1, except it is slightly larger (26 μm versus 18–23 μm) and more distinctly reticulate.

SAPINDACEAE

Cardiospermum (Fig. 72). Oblate, amb triangular; triporate, pores protruding ca. 3–4 μm, 1–2 μm diam., equatorially arranged, equidistant, aspidate, vestibulate; tectate-perforate, wall relatively thin (ca. 1.5 μm); reticulate, muri equal to or slightly broader than diameter of lumen, giving punctate effect to portions of the exine; 45 μm.

Cardiospermum is a genus of about 14 species of herbaceous, annual or perennial vines widely distributed in tropical America and in Africa. Two species are currently known from Panama (*C. grandiflorum* Swartz, *C. microcarpum* H.B.K.), and another (*C. halicacabum* L.) likely occurs there (Croat, 1976). As noted by Muller (1981), *Cardiospermum* pollen has been mentioned in the Tertiary fossil record (e.g., Leopold & MacGinitie, 1972, Eocene, Rocky Mountain region) but without documentation (description or illustration). Bartlett and Barghoorn (1973) record the genus from the Quaternary of Panama.

Paullinia (Figs. 70, 71). Oblate, amb triangular; triporate, pores 3–4 μm, equatorially arranged, equidistant; tectate-perforate, wall 2–3 μm thick; finely reticulate; 45 μm.

Paullinia is a genus of scandent shrubs or lianas widely distributed in tropical America, with one species in Africa (*P. pinnata* L.). It is most characteristic of moist forest types. About 194 species are listed for the neotropics, and Croat (1976) recorded 37 for Panama. Pollen of the genus is known from the upper Miocene of Veracruz, Mexico (Graham, 1976) and from the Quaternary of Panama (Bartlett & Barghoorn, 1973). The Gatuncillo occurrence extends the stratigraphic record of *Paullinia* back to the upper Eocene.

Serjania (Figs. 73, 74). Oblate, amb triangular; tricolporate, colpi narrow, straight, 4–6 μm long, inner margin entire to minutely dentate, equatorially arranged, meridionally elongated, equidistant, pores slit-like, situated at midpoint

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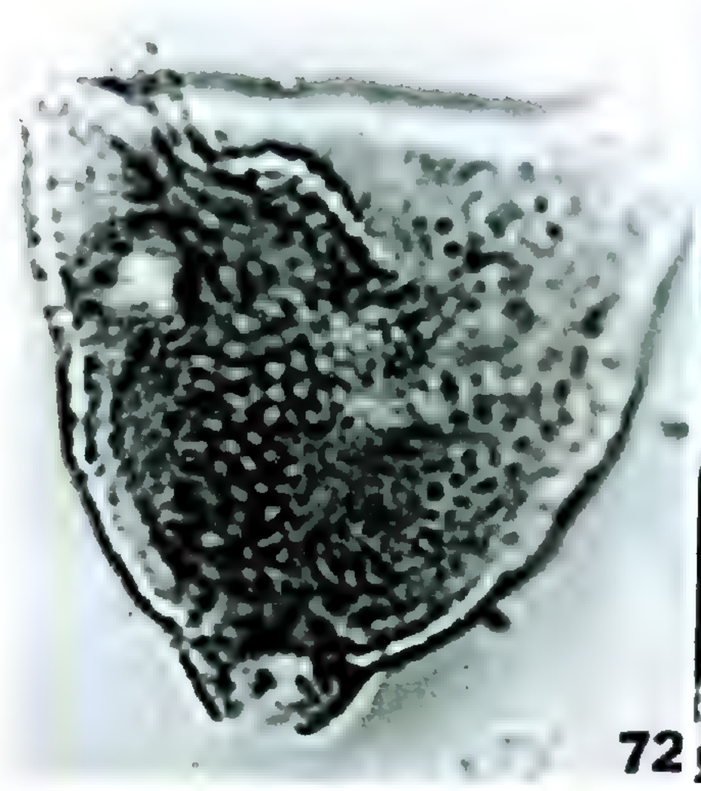
FIGURES 72–89. 72. *Cardiospermum,* 4-1, D-38,1.—73, 74. *Serjania,* 4-1, S-22,1.—75, 76. *Mortoniodendron,* 4-1, F-36,3-4; 2-1, M-39,2.—77, 78, 80. *Pelliceria,* 4-1, T-37,1; 4-1, S-27,1.—79. cf. *Chrysophyllum,* 4-1, S-19,2.—81. Unknown 3, 4-1, K-25,2.—82, 83. Unknown 5, 4-1, P-22,4.—84. Unknown 1, 4-1, X-9,2-4.—85. Unknown 2, 4-1, C-19,3.—86, 87. Unknown 7, 9-1, X-35.—88. Unknown 4, 2-1, M-28,4.—89. Unknown 6, 9-1, K-43,1.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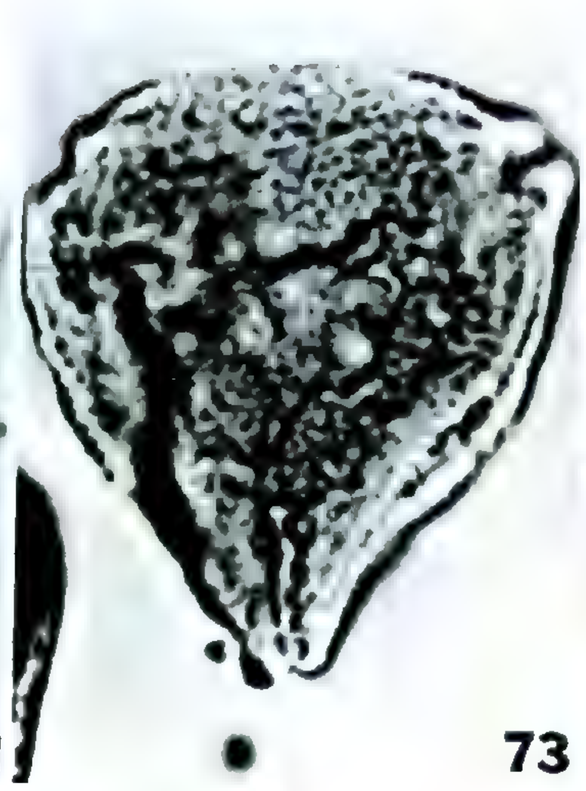
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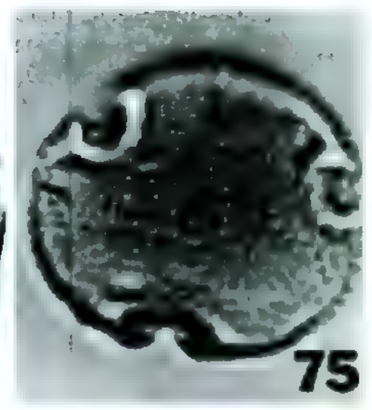
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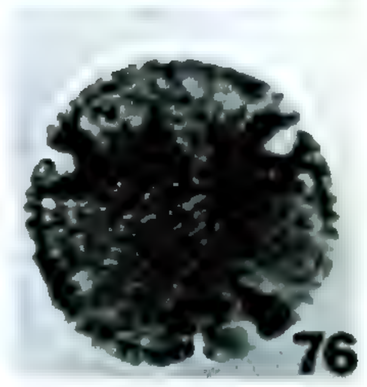
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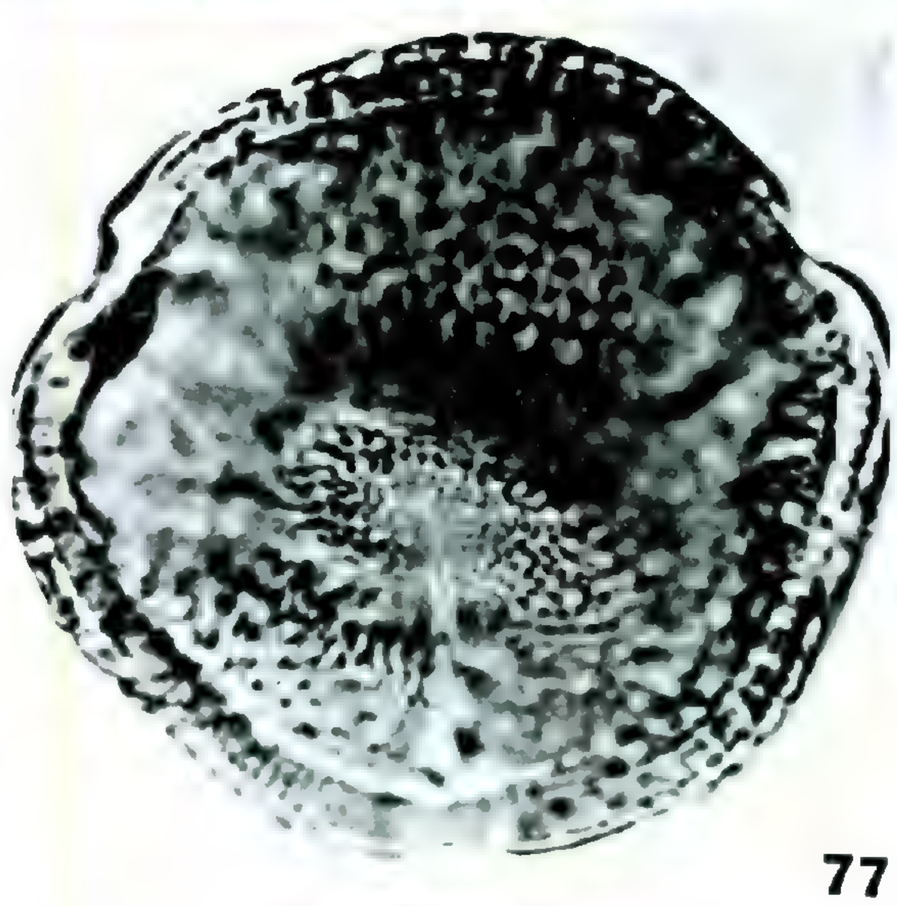
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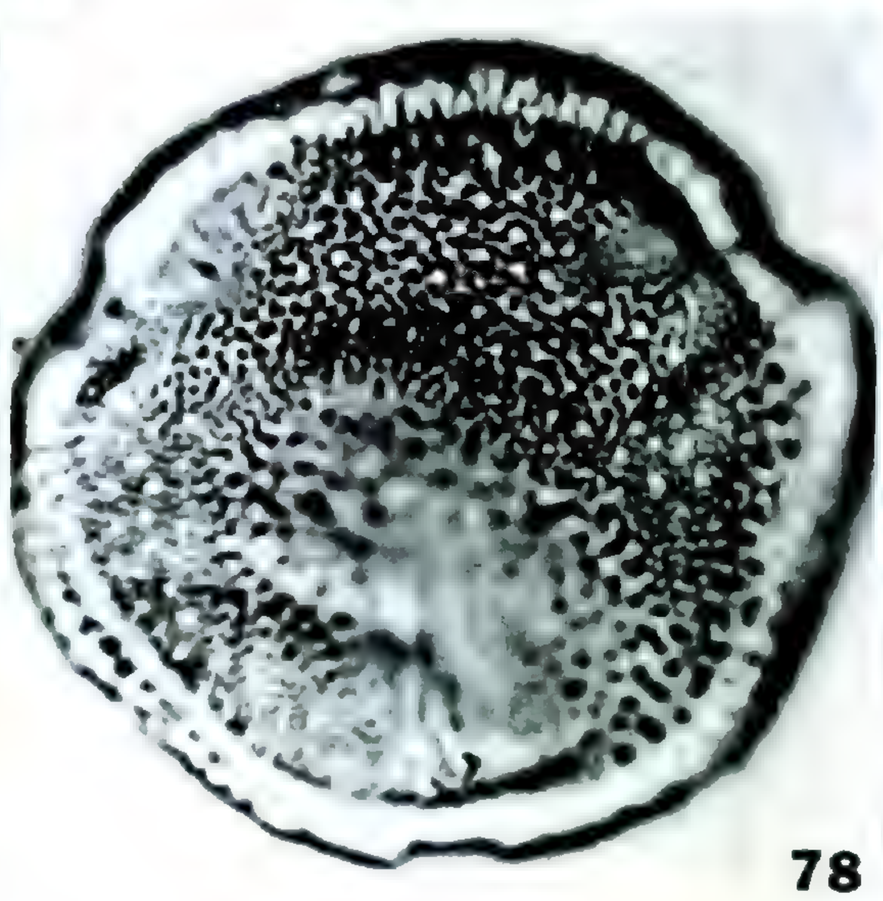
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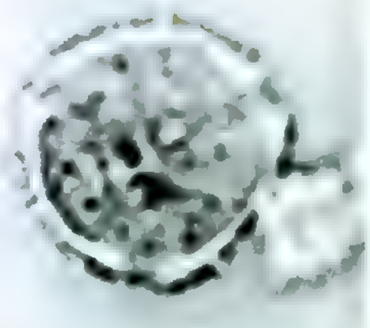
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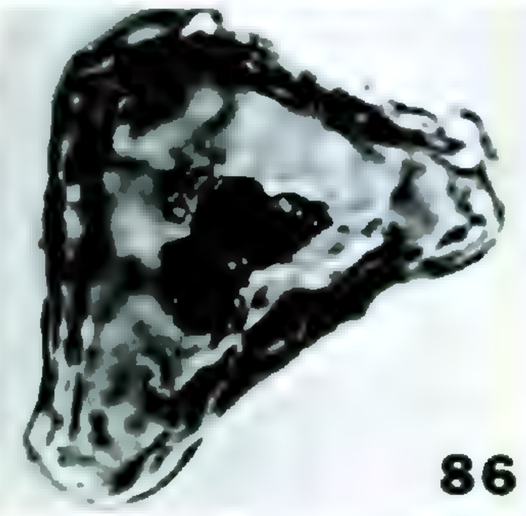
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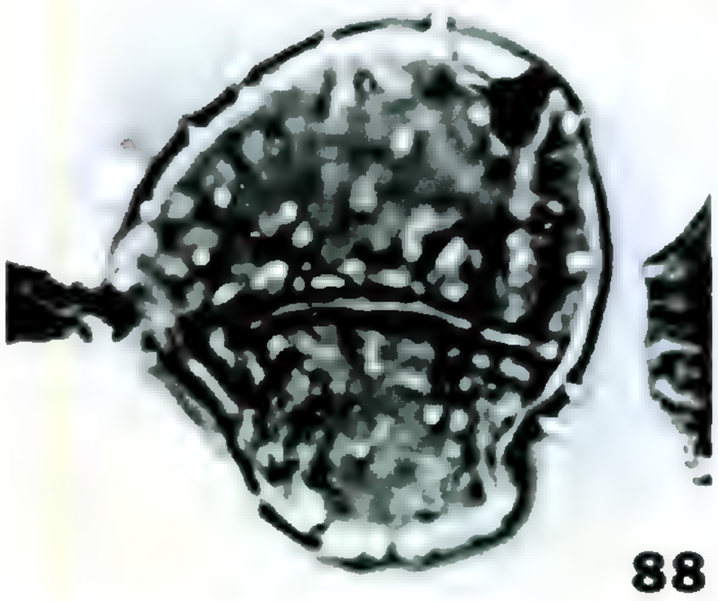
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of colpus; tectate-perforate, wall ca. 2 μm thick; finely reticulate; 45 μm.

This genus consists of about 215 species distributed from southern United States to tropical South America. The plants are scandent shrubs or lianas and occur in a wide variety of habitats. Fifteen species are listed for Panama (Croat, 1976). Pollen of *Serjania* is known from the upper Miocene of Veracruz, Mexico (Graham, 1976) and from the Quaternary of Panama (Bartlett & Barghoorn, 1973). The Gatuncillo occurrence extends the range of the genus back to the upper Eocene. Among modern species, the microfossils are similar to *S. conigera* Turcz. of the tropical moist forest.

SAPOTACEAE

cf. *Chrysophyllum* (Fig. 79). Prolate, tricolporate, colpi long (25–27 μm), narrow, straight, inner margin minutely dentate, equatorially arranged, meridionally elongated, equidistant, costae colpi ca. 1–2 μm wide, pore elongated equatorially (colpi transversalis), ca. 1 μm by 8–10 μm, inner margin entire, situated at midpoint of colpus; tectate, wall 2.5 μm thick; psilate to faintly scabrate; 52–54 μm by 28–32 μm.

Chrysophyllum is a large genus of tropical trees (150 species), especially well-represented in the American tropics. The microfossils are similar to several genera of the Sapotaceae (e.g., *Micropholis, Pouteria*) but more commonly resemble *Chrysophyllum* in quantitative details; hence, the designation cf. *Chrysophyllum*. There is considerable range in size among the species (18–46 μm in length), and a smaller form (13.5 μm by 18.9 μm) is reported from the middle Oligocene San Sebastian Formation of Puerto Rico (Graham & Jarzen, 1969). The Gatuncillo specimens are larger (52–54 μm) and extend the range of this pollen type from the middle Oligocene to the upper Eocene.

THEACEAE

Pelliceria (Figs. 77, 78, 80). Oblate, amb oval-triangular to nearly circular; tricolporate, colpi narrow, straight, 15 μm (equator to apex) (P.I. 0.4), inner margin entire, equatorially arranged, meridionally elongated, equidistant, colpi transversalis 1 μm by 12–14 μm, situated at midpoint of colpus; tectate to tectate-perforate, wall thick (7–10 μm), separation of ektexine from endexine clearly evident on most specimens; sculpture variable from mound-like clusters (verrucae) with subreticulum, to distinctly reticulate; size variable, ca. 50–70 μm.

The pollen morphology and fossil record of *Pelliceria* has been summarized by Graham (1977). Although presently confined to lowland, coastal areas from Costa Rica to northwestern Colombia, the genus is widespread in Caribbean Tertiary deposits. In the stratigraphic literature the specimens are referred to the form-genus *Psilatricolporites crassus* van der Hammen & Wymstra. It is known from the lower middle Eocene of Jamaica, upper Eocene of Panama, middle Oligocene of Puerto Rico (Graham & Jarzen, 1969), Oligo-Miocene of Chiapas, Mexico (Langenheim et al., 1967), and the Tertiary of the Guiana Basin (van der Hammen & Wymstra, 1964). A notable feature of modern *Pelliceria* pollen is the extensive range in size and sculpture patterns, which is also matched by the microfossils. Pollen of *Pelliceria* is common in the Gatuncillo Formation and was probably an important component of the fringing mangrove vegetation.

TILIACEAE

Mortoniodendron (Figs. 75, 76). Peroblate, amb oval-triangular to circular; tricolpate, colpi short (3 μm equator to apex), apices ca. rounded, inner margin entire, equatorially arranged, meridionally elongated, equidistant, conspicuous costae colpi ca. 1.5–2 μm wide; tectate-perforate; finely reticulate, reticulum closed, regular, muri ca. 0.5 μm wide, straight, surface psilate, margins entire; 23–32 μm.

Pollen of *Mortoniodendron* and its fossil record has been summarized by Graham (1979b). In that report microfossils had not been recovered from the Gatuncillo Formation, so these specimens represent new occurrences in the Caribbean Tertiary. Other records include the middle Miocene Gatun Formation of Panama (Graham, 1979b), the upper Miocene Paraje Solo Formation of Veracruz, Mexico (Graham, 1976), and the Quaternary of Panama (Bartlett & Barghoorn, 1973). Similar fossils have been reported by Tschudy and van Loenen (1970) under the name *Tiliaepollenites* from the upper Eocene of Mississippi. The complete stratigraphic range, as presently known, is upper Eocene to Recent. There are about five species of these small shrubs to tall trees growing from southern Mexico through Central America. They are most characteristic of tall moist forests. The diversity in

fossil pollen illustrated by Graham (1979b) suggests that other species or related taxa may yet be described from modern tropical forests.

UNKNOWNS

In addition to these specimens, there are others in the Gatuncillo Formation for which biological affinities are unknown. The number of such specimens increases with age of the strata, and the point at which most fossil pollen cannot be referred to a modern genus or family is frequently in a broad transition zone between the upper and middle Eocene. Consequently, the upper Eocene microfloras include a mixture of specimens that can be referred to modern genera or families, depending on the amount of variation in the modern analogs (the 'knowns'); others for which modern representatives simply have not yet been encountered in the reference collection or literature (the unknowns); and a substantial number that are not known to match the pollen of any extant taxa and probably represent extinct forms (the unknowables). The last decrease upward toward the Oligocene and younger strata, and increase below the upper Eocene to the point that they begin to significantly hamper the reconstruction of paleocommunities and paleoenvironments is based on fossil palynomorphs. Reworked palynomorphs, which can be a special problem in lignites, further complicate the assemblage although these can usually be recognized by their corroded appearance, darker color, and/or distinct morphology (especially if redeposited from Paleocene or older sediments).

The most common unknowns from the Gatuncillo Formation are illustrated in Figures 81–144 and briefly described below. These undoubtedly include both extinct forms and those for which biological affinities will ultimately be established in future studies.

UNKNOWN ECHINATE TYPES

Type 1 (Fig. 84). Spherical, amb circular; nonaperturate; tectate, wall 1 μm thick; echinate, spines ca. 1 μm, evenly spaced, moderately dense (1.5–2 μm between spines); small (10 μm).

Type 2 (Fig. 85). Oblate, amb oval-triangular; tricol(poroid?)ate, colpi ca. 3 μm wide at equator, tapering to acute apex, 6–7 μm long (P.I. 0.2), inner margin entire, equatorially arranged, meridionally elongated, equidistant; tectate, wall 1.5 μm thick; echinate, echinae short (2 μm), acute, some slightly curved, ca. evenly spaced, moderately dense (ca. 3 μm between spines); 18 μm.

Type 3 (Fig. 81). Spherical, amb circular; nonaperturate (possibly monocolpate?); tectate, wall 1.5–2 μm thick; echinate, echinae short (2 μm), blunt, ca. evenly spaced, moderately dense (ca. 3 μm between spines); 23 μm.

Type 4 (Fig. 88). Spherical, amb circular; nonaperturate; tectate, wall 1.5 μm; echinate, echinae short (2–4 μm), longer ones curved, acute, widely spaced (6–7 μm); 39 μm.

Type 5 (Figs. 82, 83). Prolate; tricol-(poroid?)ate; colpi 18–20 μm long, inner margin entire, equatorially arranged, meridionally elongated, equidistant, possibly slight costae colpi; tectate, wall thick (3–4 μm), separation of ektexine and endexine clearly evident; minutely echinate; 27 μm.

UNKNOWN INTECTATE TYPE

Type 6 (Fig. 89). Spherical, amb circular; nonaperturate; intectate, columellae short, moundlike, slightly elongated baculae, some constricted at base (clavae/gemmae), diam. of sculpturing elements 2–4 μm, smooth, some ca. hyaline, moderately dense (2–4 μm between sculpturing elements); 40 μm.

UNKNOWN TRIANGULAR TYPE

Type 7 (Figs. 86, 87). Oblate, amb triangular, outer margin undulating; triporate, pores circular, diam. 4–5 μm, inner margin entire, situated at apices of triangular grain, equidistant; tectate, wall thick (ca. 3 μm), separation of ektexine and endexine evident; psilate to faintly scabrate, some coarser, irregular sculpturing elements evident in equatorial region near pores; 31 μm.

UNKNOWN OBLATE/OBLATE-SPHEROIDAL TYPES

Type 8 (Figs. 90, 91). Oblate-spheroidal, amb ca. circular; tricolpate, colpi 34 μm long (full length), inner margin entire, slight margo formed by diminution of reticulum along colpus margin, equatorially arranged, meridionally elongated, equidistant; tectate-perforate, wall 2 μm thick; reticulate, reticulum closed, muri thin, smooth, slightly sinuous, diam. of lumen ca. 4 μm; 36 μm.

Type 9 (Figs. 92–95). Oblate, amb oval-triangular; tricolpate, colpi short, approaching pores, diam. 3–4 μm, equatorially arranged, equidistant; tectate-perforate, wall 1.5 μm thick; retic-

ulate, reticulum closed, regular, muri thin, smooth, diam. of larger lumen ca. 3 μm; 20–22 μm.

The specimen in Figures 94 and 95 may be a slightly flattened, corroded form of the specimen in Figures 92 and 93. They are representative of rubiaceous types of pollen common in the Gatuncillo Formation.

Type 10 (Figs. 96, 97). Oblate, amb circular; tricolporate, colpi faint, 14–16 μm, equatorially arranged, meridionally elongated, equidistant, pore large (diam. 8–10 μm), situated at midpoint of colpus; tectate-perforate, wall 2.5 μm thick; reticulate, reticulum closed, ca. regular, muri thin, smooth, diam. of larger lumen ca. 2 μm; 33 μm.

Type 11 (Figs. 98, 99). Oblate, amb circular; triporate, pores circular, 2.5 μm, narrow annulus, inner margin entire, equatorially arranged, equidistant; tectate, wall 1.5 μm thick; scabrate (possibly microreticulate); 22 μm.

Type 12 (Fig. 100). Oblate, amb circular; tricolpate, colpi 10 μm, extending within 4 μm of pole (P.I. 0.2), tapering to acute apex, inner margin minutely dentate, equatorially arranged, meridionally elongated, equidistant; tectate-perforate, wall 1–1.5 μm thick; finely reticulate; 20 μm.

Type 13 (Fig. 101). Oblate, amb circular; tricolporate, colpi 5–6 μm, extending within 5 μm of pole (P.I. 0.2), apex acute, inner margin entire to minutely dentate, equatorially arranged, meridionally elongated, pore conspicuous, diam. 3 μm, narrow annulus ca. 1 μm; tectate-perforate, wall 1.5 μm thick; finely and regularly reticulate; 23 μm.

Type 14 (Fig. 102). Oblate, amb triangular; tricolporate, colpi short (3–4 μm), narrow (P.I. 0.2), tapering to acute apex, inner margin entire, equatorially arranged, meridionally elongated, equidistant, pore elongated equatorially, 1 μm by 3 μm, situated at midpoint of colpus; tectate, wall 1.5 μm thick; psilate (punctations, possibly artifacts); 13 μm.

Type 15 (Fig. 103). This grain is similar to Unknown 14 except it is more oval-triangular, the wall is slightly thinner, and the surface appears more sculptured (faintly rugulate, possibly some punctations).

Type 16 (Figs. 104, 105). Oblate-spheroidal, amb circular; tricolporate, colpi long (12 μm), narrow, inner margin entire, equatorially arranged, meridionally elongated, equidistant, narrow costae colpi, pore elongated equatorially, situated at midpoint of colpus; tectate-perforate, wall 1.5–2 μm thick; reticulate, reticulum closed, regular, diminishing along colpus (faint margo), muri smooth, equal in diam. to lumen (ca. 1 μm) giving punctate effect, appearing ca. linearly aligned; 18 μm.

Type 17 (Fig. 106). Oblate, amb circular; tricolpate, colpi 12 μm, tapering to acute apex, straight, inner margin ca. entire, extending within 6 μm of pole (P.I. 0.2), equatorially arranged, meridionally elongated, equidistant; intectate, columellae thin needle-like baculae, some slightly clavate; ca. 2 μm long; 30 μm.

Type 18 (Figs. 107, 108). Oblate, amb circular; tricolpate, colpi 10 μm long, extending within 6 μm of pole (P.I. 0.2), tapering to acute apex, inner margin minutely dentate, equatorially arranged, meridionally elongated, equidistant; tectate-perforate, wall thin in relation to diam. of grain (1–1.5 μm); reticulate, reticulum closed, regular, width of muri and diam. of lumen ca. 1 μm; 30 μm.

Type 19 (Fig. 109). Oblate, amb circular to oval-triangular; triporate (short colpi), pores slightly elongated meridionally, 1 μm by ca. 3 μm, inner margin entire, conspicuous costae pori (colpi) 2.5 μm wide, pores equatorially arranged, equidistant; tectate-perforate, wall 1.5 μm thick; reticulate, reticulum regular, closed, moderately fine (diam. of lumen 1–2 μm); 27 μm.

Type 20 (Fig. 111). Oblate, amb oval-triangular; tricolporate, colpi short, faint, equatorially arranged, meridionally elongated, equidistant, pores elongated equatorially (1 μm by 3 μm), situated at midpoint of colpus, costae pori, slightly

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FIGURES 90–123. 90, 91. Unknown 8, 4-1, W-9,1.—92–95. Unknown 9, 4-1, N-15; 4-1, W-23,1-3.—96, 97. Unknown 10, 9-1, D-35,1.—98, 99. Unknown 11, 4-1, E-30,1.—100. Unknown 12, 4-1, N-10,2-4.—101. Unknown 13, 4-1, S-23,1-3.—102. Unknown 14, 9-1, J-18,3.—103. Unknown 15, 4-1, W-27,2.—104, 105. Unknown 16, 4-1, T-40,2.—106. Unknown 17, 4-1, E-28,1-2.—107, 108. Unknown 18, 4-1, S-8,3.—109. Unknown 19, 2-1, O-24.—110. Unknown 22, 4-1, O-24.—111. Unknown 20, 2-1, T-17,1-3.—112, 113. Unknown 21, 4-1, E-33,2.—114, 115. Unknown 23, 4-1, H-13,2-4.—116. Unknown 24, 4-1, V-34,1-2.—117. Unknown 25, 1-4, N-28,2-4.—118, 119. Unknown 26, 4-1, V-42.—120, 121. Unknown 27, 4-1, Q-27,1.—122, 123. Unknown 28, 4-1, K-31.

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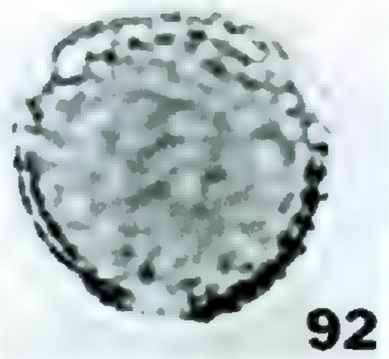
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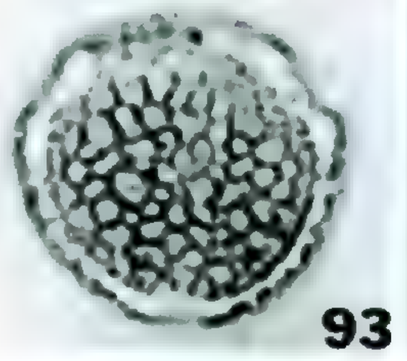
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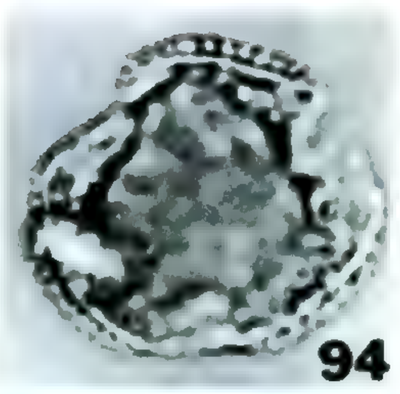
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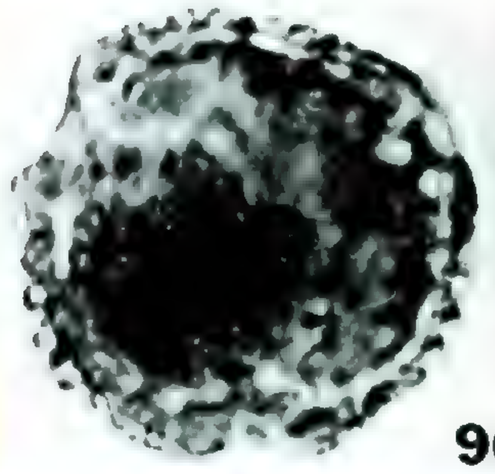
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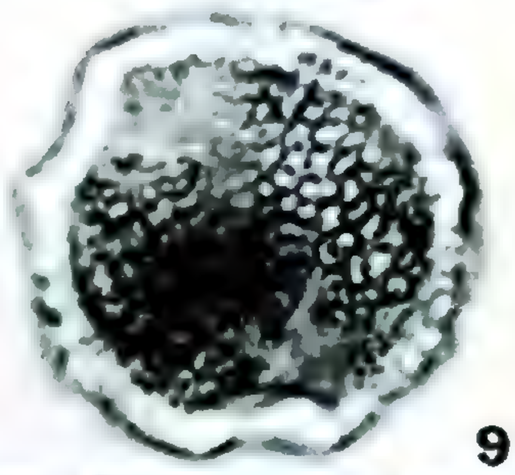
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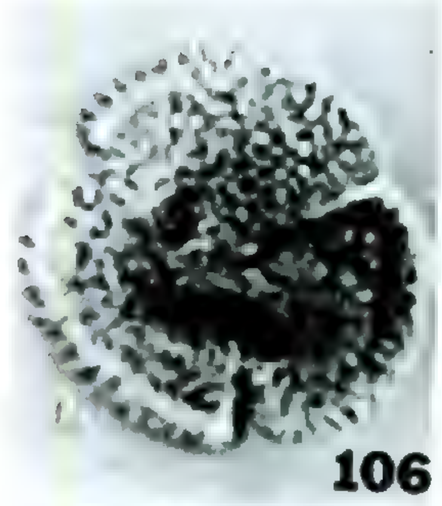
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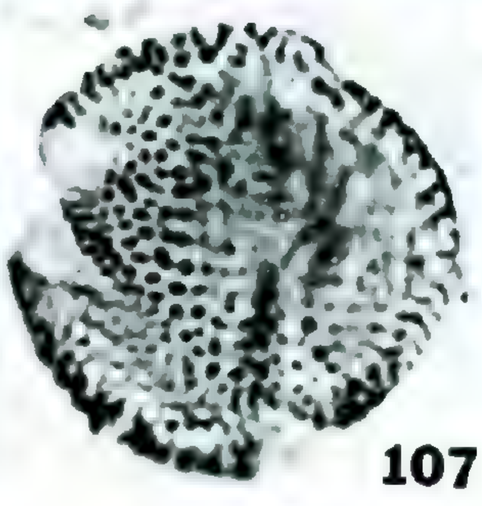
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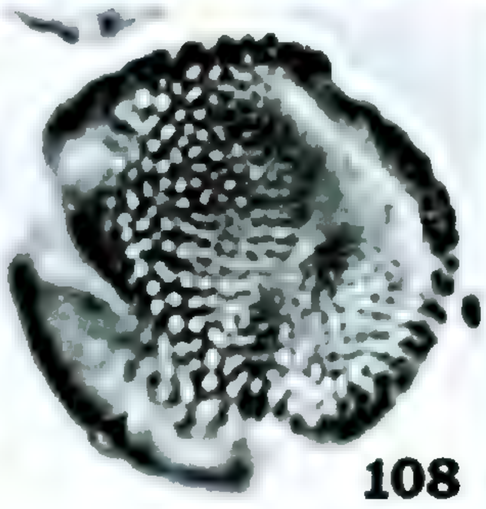
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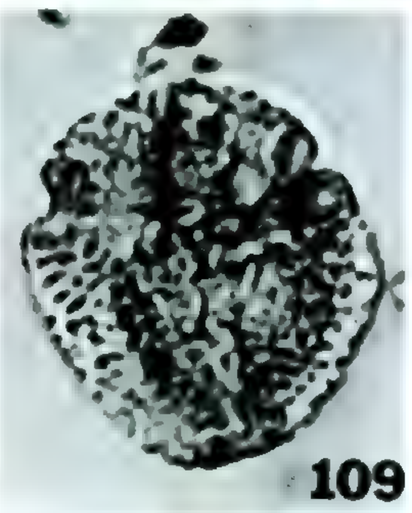
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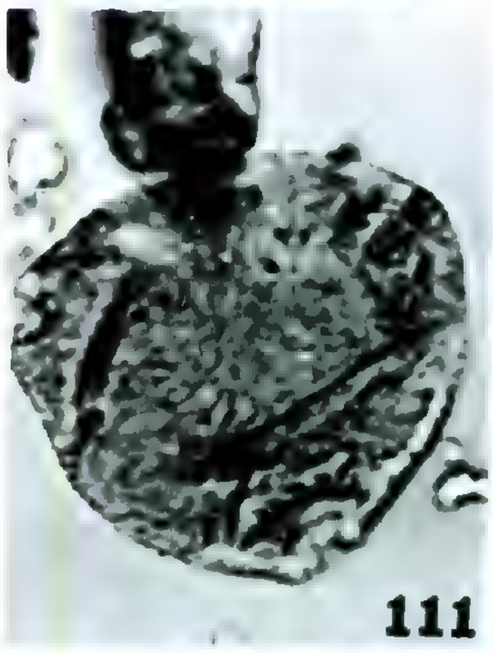
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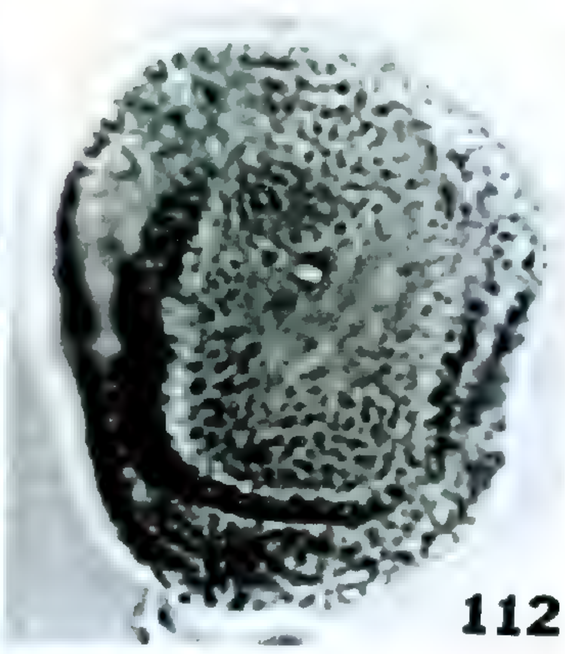
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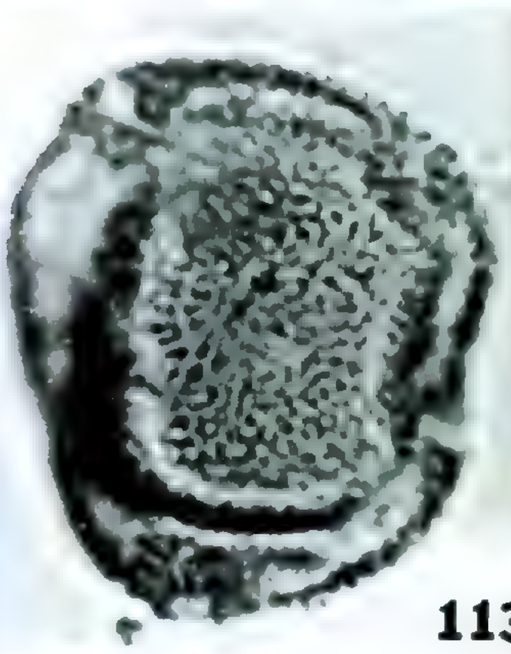
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aspidate; tectate, wall 1.5 μm thick; rugulate-striate; 32 μm.

Type 21 (Figs. 112, 113). Oblate, amb ca. circular; stephanoporate (short colpi; 5 in number), pores slit-like, equatorially arranged, equidistant; tectate-perforate, wall thin (1.5 μm); finely reticulate; 40 μm.

UNKNOWN PROLATE, TRICOL(POR)ATE TYPES

Type 22 (Fig. 110). Prolate; tricolpate, colpi long (24 μm), narrow, straight, apices acute, inner margin entire to minutely dentate, equatorially arranged, meridionally elongated, equidistant; tectate, wall 1.5 μm thick; psilate to faintly scabrate; 27 μm by 15 μm.

Type 23 (Figs. 114, 115). Prolate; tricolporate, colpi long (12 μm), narrow, straight, apices acute, inner margin entire, equatorially arranged, meridionally elongated, equidistant, pores faint, situated at midpoint of colpus; tectate, wall 1 μm thick; psilate to faintly scabrate; 15 μm by 12 μm.

Type 24 (Fig. 116). Prolate; tricolpate, colpi long (16 μm), narrow, straight, apices acute, inner margin entire, equatorially arranged, meridionally elongated, equidistant; tectate, wall 1 μm thick; faintly scabrate; 20 μm by 14 μm.

Type 25 (Fig. 117). Prolate; tricolporoidate, colpi long (16 μm), narrow, straight, inner margin entire, equatorially arranged, meridionally elongated, equidistant; tectate-perforate, reticulate, diam. of lumen ca. 1 μm; 20 μm by 18 μm.

Type 26 (Figs. 118, 119). Prolate; tricolpate, colpi long (24 μm), narrow, straight, inner margin entire to minutely dentate, equatorially arranged, meridionally elongated, equidistant; tectate-perforate, wall 2 μm thick; finely reticulate, diam. of lumen and width of muri ca. 1 μm; 27 μm by 23 μm.

Type 27 (Figs. 120, 121). Prolate; tricolporate, colpi long (18 μm), narrow, straight, inner margin entire to minutely dentate, costae colpi 2 μm wide, equatorially arranged, meridionally elongated, equidistant; tectate-perforate, wall 2 μm thick; finely reticulate, diam. of lumen and width of muri ca. 1 μm; 27 μm by 23 μm.

Type 28 (Figs. 122, 123). This type is similar to Unknown 27, except costae colpi are not evident.

Type 29 (Figs. 124, 125). Prolate; tricolporate, colpi long (18 μm), narrow, straight, inner margin entire to minutely dentate, costae colpi 2.5 μm wide, equatorially arranged, meridionally elongated, equidistant, pore circular, 2 μm, inner margin entire, situated at midpoint of colpus; tectate-perforate, wall 1.5 μm thick; finely reticulate, reticulum closed, regular, diam. of lumen and width of muri ca. 1 μm; 21 μm by 18 μm.

Type 30 (Figs. 126, 127). Prolate; tricolporate, colpi long (22 μm), narrow, straight, inner margin entire to minutely dentate, costae colpi 3 μm wide, equatorially arranged, meridionally elongated, equidistant, pore slightly elongated equatorially (1.5 μm by 3 μm), situated at midpoint of colpus; tectate-perforate, wall 1.5 μm thick; finely reticulate, reticulum closed, regular, diam. of lumen and width of muri ca. 1 μm; 27 μm by 19 μm.

Type 31 (Fig. 128). This specimen is similar to Unknown 30, but slightly smaller (22 μm by 14 μm).

Type 32 (Fig. 129). Prolate; tricolpate, colpi long (28 μm), narrow, straight, inner margin minutely dentate, apices acute, membrane sparsely granular, equatorially arranged, meridionally elongated, equidistant; tectate, wall 1.5–2 μm thick; psilate to faintly striate; 33 μm by 23 μm.

Type 33 (Figs. 130, 131). Prolate; tricolpate, colpi long (32 μm), narrow, straight to slightly sinuous, inner margin minutely dentate, equatorially arranged, meridionally elongated, equidistant; tectate to minutely tectate-perforate, wall 1.5 μm (thin in relation to size of grain); very finely reticulate; 36 μm by 27 μm.

Type 34 (Fig. 132). Prolate to prolate-spheroidal; tri(to possibly tetra-)colporate, colpi long (38–40 μm), narrow, straight, apices acute, costae colpi ca. 3 μm wide, inner margin minutely dentate, equatorially arranged, meridionally elongated, equidistant, pores conspicuous, oval (13 μm by 5 μm), inner margin entire, situated at midpoint of colpus; tectate, wall 1.5–2 μm thick; minutely reticulate; 45 μm by 33 μm.

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FIGURES 124–141. 124, 125. Unknown 29, 4-1, G-8,1-3.—126, 127. Unknown 30, 4-1, V-43,1.—128. Unknown 31, 4-1, W-15,3-4.—129. Unknown 32, 4-1, E-35,2-4.—130, 131. Unknown 33, 4-1, W-23.—132. Unknown 34, 4-1, K-37,1.—133–135. Unknown 35, 4-1, N-24,1.—136, 137. Unknown 37, 2-1, R-30,1-3.—138, 139. Unknown 36, 2-1, M-35,1.—140, 141. Unknown 38, 4-1, T-22,3.

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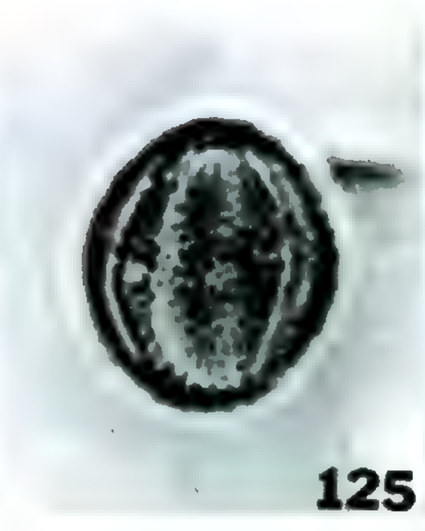
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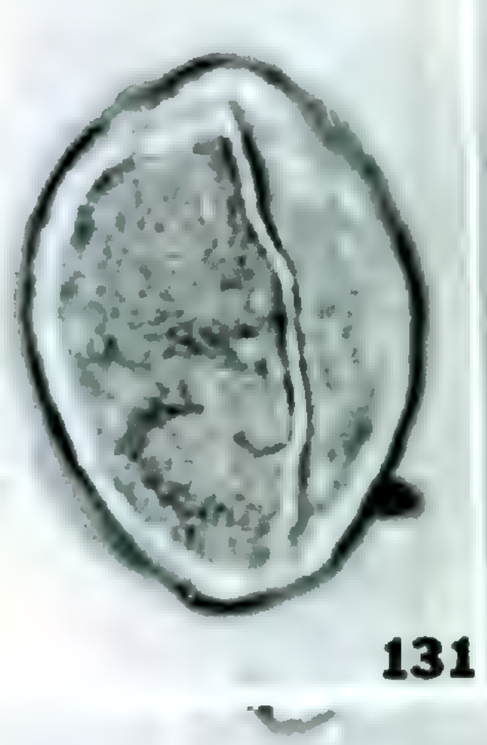
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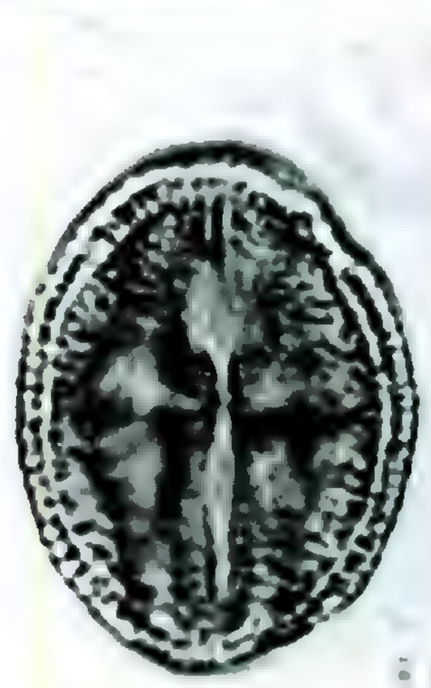
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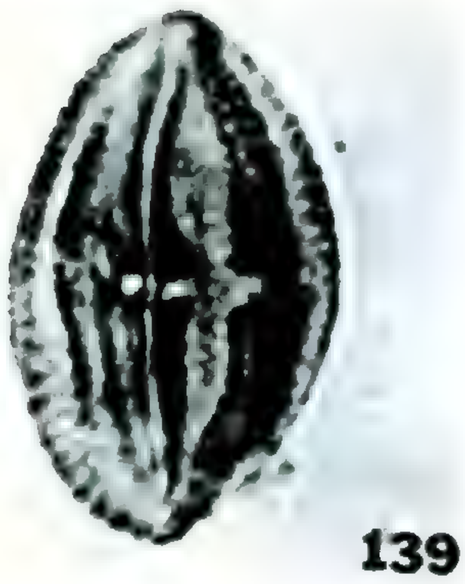
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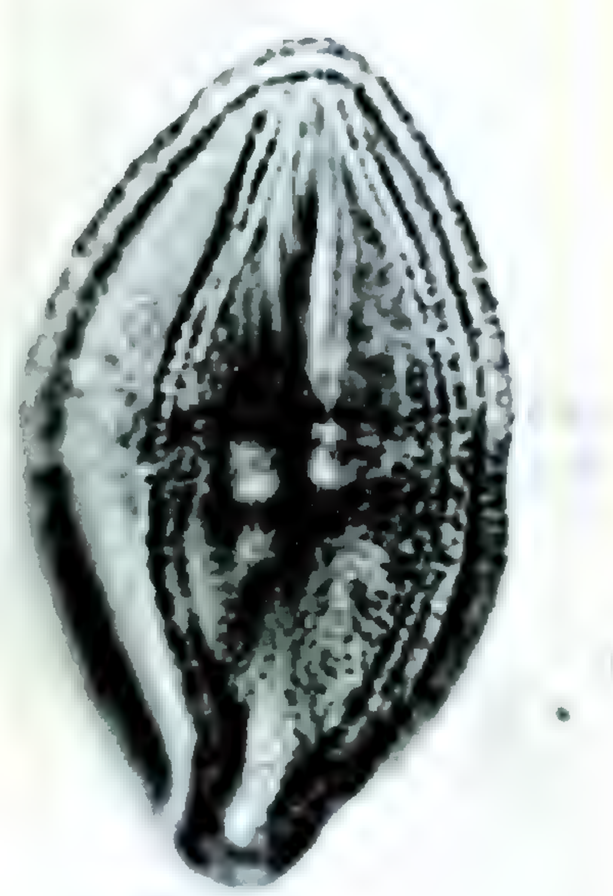
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Type 35 (Figs. 133–135). Prolate to prolate-spheroidal; tricolporate, colpi long (30 μm), narrow, straight, inner margin entire, apices acute, costae colpi 4 μm wide, pores (endoapertures) elongated equatorially (2–2.5 μm by 4–4.5 μm), situated at midpoint of colpus; tectate-perforate, wall 2.5–3 μm thick, ektexine clearly distinct from endexine; finely reticulate, diam. of lumen ca. 1 μm; 36 μm by 29 μm.

Type 36 (Figs. 138, 139). This species is similar to Unknown 35, but is slightly larger (41 μm by 24 μm) with a thinner exine (1.5–2 μm). Both are similar to several members of the Anacardiaceae but also overlap in morphology with some Euphorbiaceae.

Type 37 (Figs. 136, 137). This specimen (40 μm by 21 μm) is typical of the prolate, tricolporate, costate, reticulate type previously described, but is distinctive in that the sharp edges of the muri give a characteristic 'scooped out' appearance to the exine.

Type 38 (Figs. 140, 141). This large specimen (68 μm by 40 μm) is similar to the smaller specimens described as Unknowns 35 and 36, and resembles some Euphorbiaceae, as well as the larger Anacardiaceae. In many specimens of this type, the bases of the columellae are arranged into a subreticulum, and the wall is comparatively thick (3–3.5 μm).

Type 39 (Fig. 142). This specimen (58 μm by 40 μm) is also anacardiaceous/euphorbiaceous in aspect but has finer, more delicate columellae and a relatively thin wall (2 μm).

Type 40 (Figs. 143, 144). This specimen (68 μm by 45 μm) is of the same general type described for the Anacardiaceae/Euphorbiaceae forms but has a wall intermediate in thickness (2–3 μm) between Unknowns 38 and 39. Although these minute differences in wall thickness and columellae coarseness are difficult to quantify with exact measurements under light microscopy, such differences do impart recognizable differences between the specimens.

PALEOCOMMUNITIES

Arrangement of taxa from the Eocene Gatuncillo Formation into paleocommunities is difficult because of the age of the deposits. The microfossils represent remnants of a vegetation existing ca. 40 Ma, which was a transitional period when many lineages were differentiating into modern taxa (see previous discussion under *Tillandsia*). Consequently, the morphology of numerous specimens do not match, exactly, any modern analog, even though they may clearly be recognized as belonging to a given family. Such specimens often combine the pollen characters of two or more genera that are now palynologically distinct. This is no different in kind from similar problems encountered in younger Tertiary palynofloras; the examples just become more numerous with increasingly older deposits.

Further, it can not always be assumed that the ecological requirements of the fossil representative and its presumed modern analog are identical. This problem is lessened to some degree when paleocommunity reconstructions are based on a large number of genera, rather than on a few genera regarded as key or indicator components. The many unknowns in the Gatuncillo palynoflora also complicate interpretations.

These limitations, however, do not automatically preclude detecting the general kinds of paleocommunities present, even in late Eocene deposits. When fossil taxa cluster into community types that include many genera, based on the habitat of presumed modern analogs, it is likely that assemblage was present, even though individual components may be difficult to identify or may have changed associations through time.

Another problem involved in recognizing paleocommunities based on fossil palynomorphs is a bias toward lowland vegetation and wind-pollinated components. In tropical environments these limitations are minimized, although not eliminated, by the considerable outwashing of pollen into lowland basins of deposition by high rainfall (Germeraad et al., 1968). Muller (1959) demonstrated that pollen from upland communities is readily transported into coastal environments by tropical rivers. For example, the paleocommunities represented in the lignites of the Paraje Solo Formation of Veracruz, Mexico (Graham, 1976) include lowland communities of *Rhizophora* (manglar), the mid-altitude bosque caducifolio, the higher altitude bosque de pino y encino, and the high altitude bosque de oyamel (*Abies*). Although there is some evidence that cooler temperatures shifted the vegetation zones downward (viz., the presence of *Picea* pollen in the sediments), many of these communities were still altitudinally removed some distance from the coastal basin of deposition.

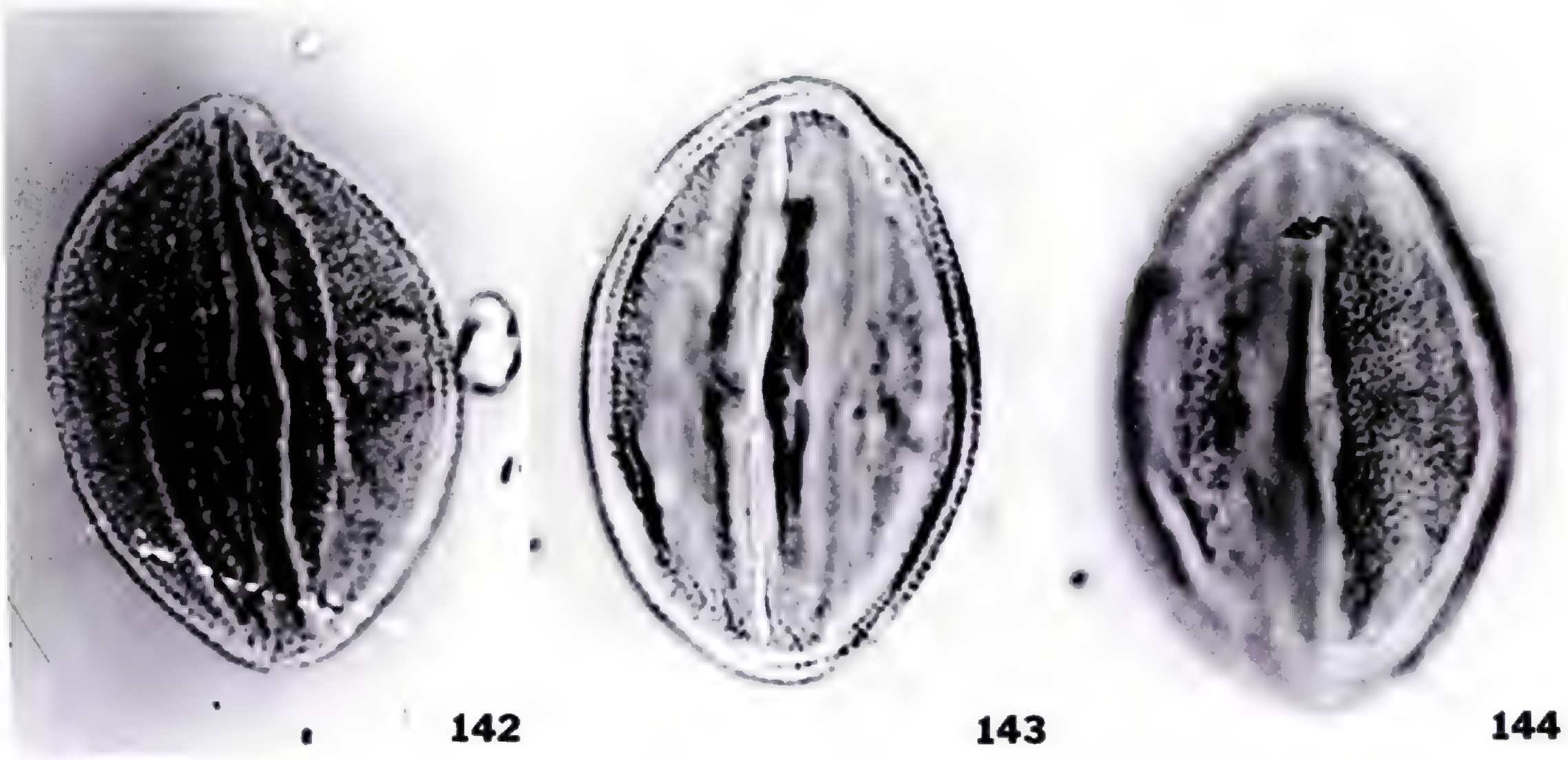
Similarly, the presence of such large, entomophilous pollen types as *Hauya* (Onagraceae, 85 μm), *Ludwigia* (Onagraceae, 104 μm), and *Hampea/Hibiscus* (Malvaceae, 135 μm) in trop-

TABLE 2. Distribution of taxa identified from the middle(?) to upper Eocene Gatuncillo Formation among comparable modern community types in Panama.

Tropical Moist Forest (21 genera + 1 widespread)
Selaginella, Ceratopteris, Pteris, Tillandsia, Campnosperma, Casearia, Chrysophyllum, Coccoloba,[b] *Combretum, Eugenia,*[c] *Faramea,*[d] *Ficus, Myrcia, Paragonia, Paullinia, Pelliceria, Protium, Rhizophora, Serjania,*[a] *Terminalia, Tetragastris, Tontalea*
Tropical Wet Forest (19 genera)
Selaginella, Pteris, Tillandsia, Casearia, Chrysophyllum, Coccoloba, Combretum, Crudia,[e] *Eugenia, Faramea, Ficus, Lisianthius,*[f] *Mortoniodendron, Myrcia, Paragonia, Paullinia, Protium, Terminalia, Tetragastris*
Premontane Wet Forest (14 genera + 1 widespread)
Selaginella, Pteris, Tillandsia, Casearia, Coccoloba, Combretum, Eugenia, Faramea, Ficus, Paragonia, Paullinia, Protium, Serjania[a]*, Terminalia, Tetragastris*
Premontane Moist Forest (3 genera + 6 widespread)
Combretum, Eugenia,[a] *Faramea,*[a] *Ficus,*[a] *Ilex, Paullinia,*[a] *Serjania, Terminalia,*[a] *Tetragastris*[a]
Premontane Rain Forest (4 genera)
Casearia, Paullinia, Serjania, Tillandsia
Tropical Dry Forest (4 genera + 2 widespread)
Cardiospermum, Casearia, Coccoloba,[a] *Combretum, Serjania, Tetragastris*[a]
Premontane Dry Forest (4 genera + 1 widespread)
Cardiospermum, Casearia,[a] *Combretum, Eugenia, Ficus*
Lower Montane Moist Forest (3 genera)
Pteris, Alfaroa, Engelhardia (*Oreomunnea*)
Lower Montane Wet Forest (2 genera)
Pteris, Tillandsia
Lower Montane Rain Forest (none)
Montane Wet Forest (none)
Montane Rain Forest (none)

[a] The genus occurs in this community but is more common or typical in other habitats.
[b] Most common in more or less stressed envirionments (swamps, beaches, limestone outcrops) but occurs in all lowland life zones.
[c] Myrtales tend to be more common in Panama in more or less stressed envrionments (e.g., Cerro Jefe) in somewhat drier forest types.
[d] The genus is most common in the tropical wet forest, but the most common species (*F. occidentalis*) is very abundant in the tropical moist forest.
[e] Most common in South America in inundated forests.
[f] Tropical wet forest, but the most common species (*L. skinneri*) is more or less weedy and occurs in drier forest types.

ical sediments (Graham, 1976; Graham & Jarzen, 1969) is witness to the effectiveness of outwashing and water transport in depositing a variety of pollen types in lowland habitats. There are obvious exceptions, such as low pollen-producing communities removed great distances from the basins of deposition (e.g., paramo), or distinctly desert communities where pollen has little chance of long-distance water transport or surviving oxidation under the arid conditions. Evidence for both vegetation types is meager in the Tertiary plant microfossil record for Latin America, but no rational interpretation of the data would automatically preclude the presence of these communities solely on the basis of the pollen record. It is becoming increasingly apparent, however, that pollen representing lowland, mid-altitude, and even high-altitude communities, including both entomophilous and anemophilous components, and wet to drier ecotypes, are commonly incorporated into lowland basins of deposition in tropical regions. Conversely, when the common and defining elements of a particular community or ecotype are consistently rare or absent in a large tropical Tertiary palynoflora, with such exceptions as noted ear-



FIGURES 142–144. 142. Unknown 39, 4-1, X-8,2-4.—143, 144. Unknown 40, 4-1, X-32,2.

lier, it is likely that assemblage was absent, poorly defined, or restricted in distribution (i.e., not a prominent component of the vegetation).

The taxa represented in the Gatuncillo Formation are arranged according to communities based on the distribution of their presumed modern counterparts (Table 2). The life-zone classification is from Holdridge (1967; Holdridge et al., 1971) and was used by Croat (1978) for describing the vegetation of Barro Colorado Island.

It is noted that the purpose of Table 2 is not to record the complete range of the genera among present-day communities in Central America. Rather, the genera are placed according to their principal or common occurrence in recognition that some are more widely distributed or may contain a species that extends beyond the range typical for the rest of the genus. Some examples are indicated by the designation (1) and by the footnotes in Table 2. In instances in which a fossil pollen type is similar to two genera (*Eugenia/Myrcia, Combretum/Terminalia*; Graham, 1980), both are listed to maximize the number of communities potentially represented in the Gatuncillo palynoflora.

When these genera are assigned to life-zones, using distributions cited by Croat (1978), family treatments in the "Flora of Panama," and comments provided by Croat and Gentry (pers. comm.), an obvious pattern emerges (Table 2). Elements from lowland, moist communities constitute the overwhelming majority in the Gatuncillo assemblage. Equally evident is the abrupt decrease in genera characteristic of 1) montane, and 2) dry forest types. Even within the constraints on interpretation previously discussed, and acknowledging that some genera range beyond the communities listed in Table 2, it is difficult to avoid the conclusion that higher altitude and drier vegetation types were poorly represented. A conservative interpretation of the existing data is that the listings in Table 2 probably reflect, in a general way, the relative importance of the paleocommunities characterizing the late Eocene landscape in this part of central Panama. The principal paleocommunities present were the tropical moist forest, tropical wet forest, and premontane wet forest. Less prominent were the premontane moist forest, premontane rain forest, tropical dry forest, and premontane dry forest, although representation in these forest types is so low, and involves primarily genera that are also found elsewhere, that some may have been poorly developed or absent. In the lower montane moist forest it is noted that *Alfaroa* and *Engelhardia* (*Oreomunnea*) are both included because the pollen cannot consistently be distinguished under the magnifications of light microscopy, and the specimens are rare in the assemblage (Table 1; ca. three specimens recovered). This forest type, together with the lower montane wet forest, lower montane rain forest, montane wet forest, and montane rain forest were probably poorly represented or absent in the re-

gion. This general reconstruction of the paleocommunities is consistent with other independent geological and paleontological evidence on paleoenvironments and paleophysiography.

Paleoenvironments

Reconstruction of paleoenvironments for the Gatuncillo flora is facilitated by information available on the geology (particularly sediment types), marine invertebrate and terrestrial mammal paleontology, and plate tectonic history of the Canal region. These data establish geological and biological parameters within which the paleobotanical results can be interpreted.

The microfossils were recovered from lignite deposits that are common in Tertiary formations throughout the Gulf/Caribbean region. The northernmost limit for any significant present-day lignite deposition in North America is southern peninsula Florida (Cohen & Spackman, 1972; Scholl, 1964a, 1964b). Thus the presence of the lignite itself suggests tropical to subtropical environments. Since these lignites commonly contain pollen of *Rhizophora, Conocarpus, Avicennia, Laguncularia,* and *Pelliceria,* this is further confirmation that the sediments reflect tropical paleoclimates. Finally, the Gatuncillo lignites are associated with coralline limestones characteristic of deposition in near-shore, tropical habitats.

Plate tectonic reconstructions show that during most of the Tertiary the present region of Panama was occupied by a series of volcanic islands located above the subduction zone between the east Pacific (Cocos) and developing Caribbean plates (Coney, 1982; Dengo, 1973). Intense tectonic activity is reflected by more than 113 faults observed within a 3 km section of the Gaillard Cut portion of the Canal (R. H. Stewart, pers. comm.). Volcanic activity is evidenced by widespread basalts, volcanic shales, and tuffs (water-lain volcanic ash) throughout the Tertiary formations of Panama (Stewart et al., 1980). A wealth of biogeographic information is consistent with a model of discontinuous land surface between North and South America during most of the Tertiary, culminating with uplift of the Panama land bridge in latest Pliocene and Pleistocene times (Graham, 1973b; Marshall et al., 1976, 1981, 1982; Raven & Axelrod, 1974; Webb, 1976; Whitmore & Stewart, 1965; Woodring, 1966). This documentation of the insular nature of the landscape is important in interpreting climatic histories because biotas of small- to moderate-sized islands are often more insulated from climatic changes than comparable biotas of inland continental areas. If these islands are of relatively low relief, climatic changes that are well-documented in paleofloras derived from continental areas of more diverse physiography (viz., like those from Veracruz, Mexico or the Andean region) may not be as evident in paleofloras derived from low-lying insular vegetation.

The palynological evidence previously discussed suggests that the Eocene landscape, in the vicinity of the Gatuncillo depositional basin, was of moderately low relief. There is no evidence for either locally deposited or long-distance wind or water transported pollen from montane communities. Equally rare is pollen from dry vegetation types.

Thus, the local paleoenvironmental setting for these late Eocene biotas appears to include a series of volcanic islands of moderate to low relief, bordered seaward by shallow limestone-depositing coralline communities, fringed by mangrove vegetation of *Rhizophora* and *Pelliceria,* supporting inland communities of tropical moist, tropical wet, and premontane wet forests, growing under the general tropical conditions of high and evenly distributed rainfall and high uniform temperatures.

These general paleoclimatic conditions under which the Gatuncillo flora existed can be refined, to some extent, by a comparison with modern communities of similar composition. Normally, communities as old as the late Eocene resemble modern assemblages of comparable habitats only in a very general way. In the case of the Gatuncillo flora, however, there is a modern analog in which virtually all the components of the paleocommunity presently grow together. Gentry (pers. comm.) noted that the fossil palynoflora shows a remarkable resemblance to the lowland, swampy, and bordering vegetation between the Atlantic side of Gatun Lake and Piña, province of Colon. This is an interesting observation since the rainfall at nearby Colon, on the Atlantic side where the vegetation shows considerable similarity to the paleocommunities, is nearly double that at Balboa, on the Pacific side where the vegetation shows distinctly less similarity to the paleocommunities (107.3" versus 68"; Croat, 1978: 3). A very general estimate of temperature regimes is provided by data from the forest floor (versus open clearings) on Barro Colorado Island in Gatun Lake (Rubinoff, 1974, cited in Croat,

1978). There the mean maximum forest floor temperature is 28.0°C and the mean minimum is 21.1°C. Although these figures provide only the most general of estimates for upper Eocene conditions in the vicinity of the Gatuncillo depositional basin, they are of interest as the first approximation of terrestrial paleoenvironments available for all of northern Latin America based on paleobotanical data. As noted earlier, the nearest Eocene floras are in South America, which during this time was isolated between Africa and North America and the Mississippi Embayment floras to the north. More precise reconstructions of regional paleoenvironments must await discovery of other fossil floras from the upper Eocene elsewhere in Central America.

Of biogeographic interest is the list of families provided by Raven and Axelrod (1974) considered to be 1) of South American origin and migrating to North America in Eocene or later times, and 2) those probably already established in North America by the late Eocene. An exact correlation would not be expected because the paleoflora is of an age and location that could preserve the earliest migrants from both continents. Nonetheless it is worthwhile to record the analyses because eventually similar information from other paleofloras, combined with biogeographic studies of the modern vegetation, will allow more precise estimates as to the region of origin of certain angiosperm families. Among the families listed by Raven and Axelrod (1974) as primarily of South American origin and migrating into North America during Eocene or later times, only four are recorded in the Gatuncillo palynoflora: Bromeliaceae, Combretaceae, Flacourtiaceae, and Malpighiaceae. Among those listed as already established in North America by the Eocene, 12 were represented in the Gatuncillo palynoflora: Anacardiaceae, Aquifoliaceae, Araliaceae, Bignoniaceae, Leguminosae (Caesalpinioideae), Moraceae, Myrtaceae, Rubiaceae, Sapindaceae, Sapotaceae, Theaceae, and Tiliaceae. At the family level the palynoflora seems to have somewhat greater affinities with North American-derived elements than with South American ones. None of the families listed by Raven and Axelrod (1974) as primarily characteristic of arid habitats in tropical America were represented in the Gatuncillo assemblage.

Genera identified from the Gatuncillo Formation that have not previously been reported in the fossil record include *Lisianthius* (Gentianaceae) and *Cardiospermum* (Sapindaceae). Three other tentative reports will have to await additional specimens, and possibly SEM/TEM studies, for confirmation. These include cf. *Paragonia/Arrabidaea* (Bignoniaceae), cf. *Tetragastris* (Burseraceae), and cf. *Tontalea* (Hippocratiaceae). All are rare in the assemblage (Table 1). Range extensions are recorded for six pollen types in the Caribbean Tertiary (based primarily on previous stratigraphic ranges summarized by Germeraad et al., 1968; Muller, 1981): *Casearia* (from middle Oligocene), cf. *Ficus* (= *Psiladispo-rites minimus*; diporate Moraceae), *Faramea* (diporate form, first report; triporate known from middle Oligocene), *Paullinia* (from upper Miocene), *Serjania* (from upper Miocene), and cf. *Chrysophyllum* (from middle Oligocene).

The next palynofloras to be treated in this study are from the Culebra, Cucaracha, and La Boca Formations exposed along the Gaillard Cut section of the Panama Canal (Graham et al., 1985). They will reflect the changes in climate, physiography, and vegetation during a 16 Ma period between the late Eocene (ca. 40 Ma) and the early Miocene (ca. 24 Ma; Harland et al., 1982).

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A NEW *CYMBOPETALUM* (ANNONACEAE) FROM COSTA RICA AND PANAMA WITH OBSERVATIONS ON NATURAL HYBRIDIZATION[1]

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ABSTRACT

Cymbopetalum torulosum G. E. Schatz, sp. nov., known from northeastern Costa Rica and a single location in Pacific western Panama adjacent to the Costa Rica border, is distinguished from the sympatric *C. costaricense* (Donn. Sm.) R. E. Fries by its strongly torulose monocarps. Populations at the La Selva Biological Station of the Organization for Tropical Studies are found on recent alluvial soils. They flower from February to August, are pollinated by the dynastine beetle *Cyclocephala sparsa* Arrow, and are dispersed by ochre-bellied flycatchers (*Mionectes oleaginea*). The species hybridizes with *C. costaricense.*

Se describe y se illustre una especie nueva de *Cymbopetalum* del nordeste de Costa Rica y de una sola localidad en Panamá, cerca de la frontera con Costa Rica al lado del Pacífico. Es muy fácil de distinguir *C. torulosum* de la especie sympátrica *C. costaricense* por medio de los monocarpos torulosos. Populaciones en la Estacíon Biología La Selva de la Organizacíon de Estudios Tropicales se encuentran en suelos recientes alluviales. Ellos florecen de Febrero hasta Agosto, estan polinizadas por el coleóptero *Cyclocephala sparsa* y estan dispersadas por el pájaro *Mionectes oleaginea.* La especie hybride con *C. costaricense.*

Cymbopetalum Bentham is one of the best circumscribed and most easily recognized genera of neotropical Annonaceae. It is characterized by the inner whorl of thick, fleshy, saccate petals. When last revised (Fries, 1931), the genus consisted of nine species ranging from Mexico to Brazil. Since that time, six additional species have been described (Schery, 1941; Fries, 1952, 1956; Lundell, 1974a, 1974b). Another distinctive species has now been discovered at La Selva Biological Station of the Organization for Tropical Studies.

Cymbopetalum torulosum G. E. Schatz, sp. nov.

TYPE: Costa Rica. Heredia: La Selva Biological Station, at the confluence of the Río Puerto Viejo and Río Sarapiquí, 3 km S of the town of Puerto Viejo de Sarapiquí, 10°26′N, 84°00′W, 35 m, 19 July 1984 (fl, fr), *Schatz & Grayum 1029* (holotype, MO; isotypes, CR, DUKE, NY, WIS.

Arbor parva usque ad 5 m alta, ramulis novellis tomentellis cinerascentibus. Folia brevipetiolata, petiolo applanato tomentello, lamina membranacea bullata, elliptica-oblonga ad obovata, 15–22 cm longa, 5–9 cm lata, apice acuminato ad caudato, basi inaequilatera rotundata ad cuneata, nervis lateralibus utrinque 17–22. Flores solitarii, penduli, supra-axillares; pedicelli tomentelli, 2–4 cm longi; sepala flavescentia, late ovata, 4–6 mm longa, 5–8 mm lata, apiculata, tomentella; petala exteriora flavescentia, plana, tenuia, late ovata, 19 mm longa, 16–19 mm lata, apiculata, tomentella, intus reticulata; petala interiora flavovirentia, crasse carnosa, cymbiformia, late ovata ad rotundata, 26–36 mm longa, 17–24 mm lata, extus sulcata. Stamina numerosa, 3.5–3.8 mm longa, filamentis 0.4 mm longis, connectivis minute papillatis. Carpella 8–24, 3 mm longa, stigmatibus connatis; ovula 8–12. Fructus apocarpus, monocarpiis usque ad 24, torulosis, 9 cm longis, apicibus acutis, stipitibus 10–15 mm longis.

Small trees to 5 m tall and 4 cm diam. at breast height. Young branches minutely gray-tomentose. Leaves alternate, short-petiolate, the petioles 2–3 mm long, flattened, tomentulose; leaf blade membranaceous, conspicuously bullate when fresh, grayish green with a slight sheen, elliptic-oblong to obovate, 15–22 cm long, 5–9 cm wide, the apex long acuminate to caudate, the base slightly inaequilateral, rounded to cu-

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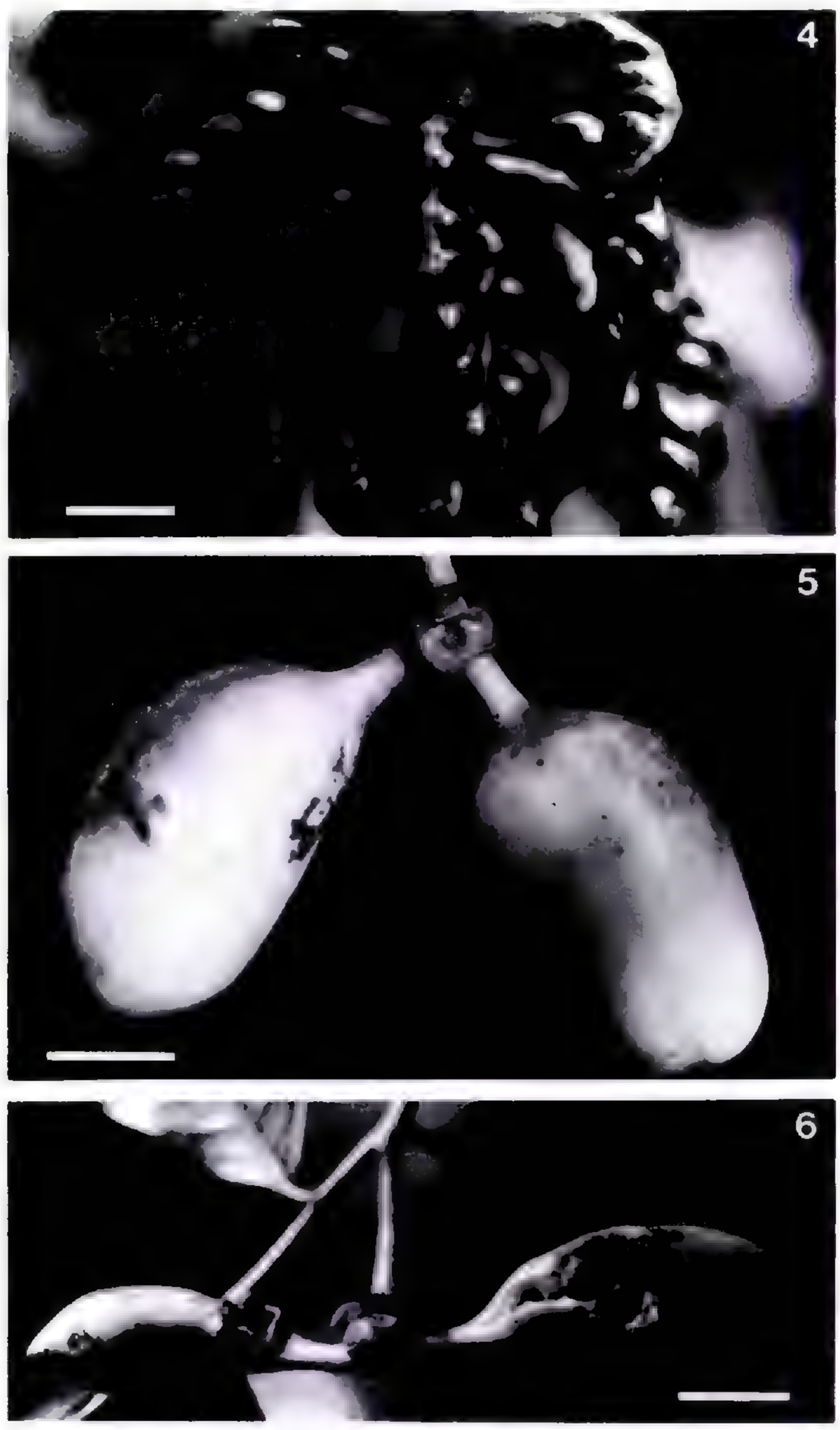
FIGURES 1–3. Flowers of Costa Rican *Cymbopetalum*.—1. *C. torulosum* at the end of female receptivity or the beginning of anther dehiscence (note closed outer petals).—2. *C. torulosum* during early female receptivity (note grooves and exudate on the stigmata). The pollinator, *Cyclocephala sparsa* Arrow (Scarabaeidae: Dynastinae), feeds at the base of one of the fleshy, inner petals.—3. *C. costaricense* during late anther dehiscence (note reflexed outer petals). Scale bar = 1 cm.



FIGURES 4–6. Fruits of Costa Rican *Cymbopetalum*.—4. *C. torulosum*.—5. *C. costaricense*.—6. Putative *C. torulosum* × *C. costaricense* hybrid (note the acute apex). Scale bar = 2 cm.

neate, the midrib sericeous on both surfaces, especially toward the base, elevated beneath, the 17–22 pairs of major lateral veins slender and strongly impressed. Flowers protogynous, actinomorphic, solitary, pendulous, supra-axillary, the pedicels rigid, minutely tomentose, especially at the base, 2–4 cm long; sepals 3, rarely 4, broadly ovate, 4–6 mm long, 5–8 mm wide, apiculate, minutely tomentose; petals 6, rarely 8, in two strongly differentiated whorls: outer petals closed down at anther dehiscence, appressed to inner petals, green initially, turning yellow at the end of female receptivity, thin, broadly ovate, 19 mm long, 16–19 mm wide, minutely tomentose, the apex acute, apiculate, the inner surface slightly reticulate; inner petals yellowish green, thick, fleshy, cymbiform, broadly ovate to rounded, 26–36 mm long, 17–24 mm wide, minutely tomentose, the margins strongly involute, 2 mm wide, the apex acute, the outer surface strongly sulcate, the inner surface only slightly striated. Stamens numerous, 3.5–3.8 mm long, the filaments 0.4 mm long, the anthers 3.1–3.4 mm long, the connectives minutely papillate. Carpels (8–)15–20 (–24), 3 mm long, the stigmata fused into a head which abscises as a unit just prior to anther dehiscence, the ovules 8–12 in a single row. Fruit

TABLE 1. Distinguishing characteristics of Costa Rican *Cymbopetalum*.

C. torulosum	*C. costaricense*
Young branches tomentulose	Young branches glabrous
Leaves elliptic-oblong to obovate, grayish green, with a slight sheen	Leaves elliptic, olive green, very glossy
Leaves with 17–22 pairs of major lateral veins, these strongly impressed, the lamina bullate	Leaves with 9–12 pairs of major lateral veins, these only slightly impressed, the lamina smooth
Flowers solitary, borne midway between nodes bearing full-sized leaves	Flowers borne on new "short-shoots," subtended by small bract-like leaves, thus clustered, and either leaf-opposed or pseudo-terminal
Calyx and corolla tomentulose	Calyx slightly tomentulose, corolla glabrate
Outer petels closed at anther dehiscence, appressed to inner petals	Outer petals usually strongly reflexed at anther dehiscence
Outer petals slightly reticulated on the inner surface	Outer petals strongly striated on the inner surface
Inner petals strongly sulcate on the outer surface, only slightly striated on the inner surface	Inner petals glabrous on the outer surface, striated on the inner surface
Monocarps torulose at maturity, the apex acute, with a single row of seeds	Monocarps not torulose at maturity, the apex rounded, with two rows of seeds

apocarpous, a cluster of up to 24 monocarps, the monocarps torulose, to 9 cm long (including stipes 1–1.5 cm long), opening along a suture which appears at maturity along the abaxial surface opposite the indehiscent carpellary suture; seeds black, ellipsoid, 12 mm long, 7 mm diam., with a thin orange aril (Figs. 1, 2, 4).

Distribution. *Cymbopetalum torulosum* is known from the Río San Juan drainage in northeastern Costa Rica, both from the Río Sarapiquí region and the Llanuras de San Carlos, and from a single specimen from lowland Chiriquí Province, Panamá, adjacent to the Costa Rican border along the Pacific coast, an area comparable in rainfall. It is also to be expected in southeastern Nicaragua, as yet a poorly collected area.

Ecology. At the La Selva Biological Station of the Organization for Tropical Studies, *Cymbopetalum torulosum* is restricted to the most recent alluvial soils bordering the Río Puerto Viejo, Río Sarapiquí, and Río Peje, and slightly

FIGURES 7, 8. Monocarps of Costa Rican *Cymbopetalum*. In each figure: left, *C. costaricense* with rounded apex; center, putative *C. torulosum* × *C. costaricense* hybrid with acute apex (note variable morphology of putative hybrid monocarps); right, *C. torulosum* with acute apex. Scale bar = 2 cm.

inland from the rivers along their tributaries and in low-lying swamps. It flowers over a long period from February to August, during the dry season and early part of the rainy season, with the peak of flowering occurring during April and May, and is pollinated by *Cyclocephala sparsa* Arrow (Scarabaeidae: Dynastinae), attracted to female phase flowers during the early evening hours by a subtle odor reminiscent of linseed oil (unpubl. data). Fruit takes six to seven months to mature before the carpels split open to reveal the orange-arillate seeds. Seeds of *C. torulosum* are dispersed by birds that feed upon the aril and either pass or regurgitate the seeds. Regurgitated *Cymbopetalum* seeds have been recovered from an ochre-bellied flycatcher (*Mionectes oleaginea*), an apparent specialist on arillate seeds (D. Levey, pers. comm.). Seeds germinate in approximately four weeks (unpubl. data).

Etymology. From the Latin *torulosus,* meaning cylindrical with constrictions at intervals, and referring to the strongly torulose monocarps, distinguishing them from monocarps of the sympatric *C. costaricense* (Donn. Sm.) R. E. Fries (Figs. 3, 5).

Specimens examined. COSTA RICA. HEREDIA: La Selva Biological Station, confluence of the Río Puerto Viejo and Río Sarapiquí, 10 May 1982 (fl), *Schatz 589* (WIS); 7 Apr. 1982 (fl), *Hammel 11607* (CR, DUKE, WIS); 16 July 1981 (fr), *Hammel 10990* (DUKE); 14–17 June 1968 (fl), *Burger & Stolze 5747* (F, NY); 26 Apr. 1973 (fl), *Burger & Gentry 9248* (F); 27 Apr. 1981 (fl), *Folsom 9879* (DUKE, WIS); 25 May 1982 (fl), *Hammel 12499* (DUKE, WIS); 23 Apr. 1982 (fl), *Hammel & Trainer 12753* (DUKE, WIS). ALAJUELA: near Caño Negro, 18–22 km N of Agua Zarcas in Llanuras de San Carlos (10°31′N, 84°24′W), 60 m, 21 May 1968 (fl), *Burger & Stolze 5200* (F). PANAMA. CHIRIQUÍ: Comarca del Baru, area W of Puerto Armuelles, 100 ft., 15 June 1957 (fl), *Stern & Chambers 127* (MAD).

There appears to be a natural subdivision within *Cymbopetalum* between torulose and non-torulose fruited species. *Cymbopetalum torulosum* is more closely related to the other torulose-fruited species than to the sympatric *C. costaricense,* from which it is easily distinguished (Table 1). Within the torulose-fruited group, *C. torulosum* seems to be most closely related to *C. tessmannii* R. E. Fries from Peru. It differs from *C. tessmannii* by having larger leaves with more major lateral veins, larger flowers, and more ovules per carpel.

Determination of Costa Rican *Cymbopetalum* becomes problematic in light of the discovery of hybridization between *C. torulosum* and *C. costaricense* at La Selva Biological Station. *Cymbopetalum torulosum* is restricted to the most recent alluvial soils; *C. costaricense* occurs on older alluvium and residual soils. Putative hybrid individuals have been located in a zone of overlap, where the most recent alluvium grades into older alluvium. Flowering phenology of the two species also differs at La Selva. Peak flowering of *C. torulosum* occurs during April and May, whereas that of *C. costaricense* occurs in July and August. Nevertheless, overall flowering periods of each species do overlap. *Cymbopetalum costaricense* is also pollinated by *Cyclocephala sparsa,* and marked individuals of *C. sparsa* have been observed to move from one species to another within a 24 hour period.

Putative hybrids are intermediate in both vegetative and reproductive characters, such as the amount of pubescence on young branches and the number of major lateral veins on leaves. The fruits of hybrids are particularly illustrative, the monocarps exhibiting two rows of seeds, one complete and the other incomplete, and always having an acute apex (Figs. 6–8). The morphology of hybrid fruits is variable, the monocarps often resembling more closely one or the other of the parental types (Figs. 7, 8).

Artificial interspecific crosses have yielded mature fruit and seed (unpubl. data). Seeds from the spontaneous putative hybrid fruit pictured in Figures 6 and 7 germinated successfully.

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NOTES ON AND DESCRIPTIONS OF SEVEN NEW SPECIES OF MESOAMERICAN CLETHRACEAE[1]

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ABSTRACT

Taxonomic confusion in Mesoamerican Clethraceae, caused by important differences between Sleumer's 1967 monograph and the 1966 "Flora of Guatemala" treatment by Standley and Williams, is resolved. Seven new species of *Clethra* are described also: three from Mexico, *Clethra breedlovei, C. oaxacana,* and *C. michoacana*; one from Nicaragua, *C. nicaraguensis*; one from Costa Rica, *C. talamancana*; and two from Panama, *C. tutensis* and *C. coloradensis.*

The genus *Clethra* Gronov. ex L. comprises approximately 70 species, of which about 40 are neotropical (Sleumer, 1967). Sleumer (1967) wrote his monograph of the genus at the same time that Standley and Williams (1966) prepared their treatment of Clethraceae for the "Flora of Guatemala." Standley and Williams (1966: 74) stated that "many of Dr. Sleumer's annotations are accepted here but others are not." The disagreements and resulting taxonomic confusion involve several widespread species that are treated under different names in the two treatments. In an earlier work on the family, Britton (1914) recognized many more distinct species than subsequent authors have thought warranted (Standley & Williams, 1966; Sleumer, 1967; Robertson, 1968).

In preparing Clethraceae for "Flora de Nicaragua" (Hamilton, in prep.), I have attempted to reconcile these differences in order to identify the many specimens collected since 1965. The major differences between Sleumer (1967) and Standley and Williams (1966) are considered below, and recommendations and additions are made where appropriate. Solutions to these taxonomic problems are especially important because the species in question account for approximately 70% of Central American material of *Clethra.* Complete keys to the Mesoamerican species will be included in the "Flora Mesoamericana" treatment of the family (Sutton, in prep.). I examined 75 sheets at MO, the duplicates of which were cited by Sleumer, especially closely. Additional material from F, HNMN, and MO was studied.

LEGITIMACY OF *CLETHRA OCCIDENTALIS*

Standley and Williams (1966) doubted the legitimacy of the combination *Clethra occidentalis* (L.) O. Ktze., noting that Kuntze (1898) did not cite the basionym. As Sleumer (1967) correctly pointed out, however, the transfer was legitimately accomplished earlier by Kuntze (1891), who clearly cited the basionym, *Tinus occidentalis* L. Steudel (1821) was actually the first to use the name *Clethra occidentalis,* but he did so without citing basionym or authority.

THE *CLETHRA MACROPHYLLA* GROUP

Standley and Williams (1966) treated *Clethra macrophylla* Mart. & Gal., *C. vicentina* Standl., and *C. occidentalis* (L.) O. Ktze. as one species, *C. macrophylla,* whereas Sleumer (1967) recognized them as separate entities.

The three species appear to be closely interrelated: they share grey-brown inflorescences, usually entire leaf margins, and usually striking color differences between the dark upper surfaces and the pale lower surfaces of the leaf blades. *Clethra vicentina* is easily distinguished, however, by its glabrous leaf blades which often dry grey-green instead of dark brown above. Furthermore, material collected of both *C. vicentina* and *C. occidentalis* in Honduras and Nicaragua shows no evidence of intergradation relative to the characters mentioned above.

The distinction between *C. macrophylla* and *C. occidentalis* is more problematic. The former has longer leaf blades (15–20 cm versus 7–12 cm) and thicker, more reddish pubescence on the leaf

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undersides. The two species occur only allopatrically, however, and careful field study may reveal that they represent one variable species. *Clethra macrophylla* occurs in Mexico, Guatemala, and Costa Rica, whereas *C. occidentalis* occurs in Belize, Honduras, and Nicaragua. If they are to be considered one species, the correct name is *C. occidentalis* (L.) O. Ktze. (the specific epithet published by Linnaeus in 1759) rather than *C. macrophylla* Martens & Galeotti (1842), the name used by Standley and Williams (1966).

Standley and Williams (1966) did not mention *C. hartwegii* Britt. as growing in Guatemala. It is a chiefly Mexican species that also reaches Guatemala and is related to the species considered above. It may be distinguished from them by its short (3–4 mm), robust pedicels and the deep rust-colored tomentum on the inflorescences. Another Mexican species, *C. pringlei* Watson, also belongs in this species group.

THE *CLETHRA LANATA* GROUP

Standley and Williams (1966) treated *C. mexicana* A. DC. and *C. lanata* Mart. & Gal. as conspecific and used the former name. They are, however, distinct species. *Clethra mexicana*, which appears to be solely Mexican, has inflorescence rachises that are extremely stout, furrowed, and deep red-brown, and the fruit is large (5–6 mm diam.). *Clethra lanata*, a variable species found from Mexico to Panama, has more slender, pale brown rachises and smaller fruit (3 mm diam.).

I differ with Sleumer (1967), however, on the status of one species in this group. *Clethra rosei* Britt. appears quite distinct and striking in Mexico, with its upper leaf surfaces scabrous to pubescent and its styles usually longer than those of *C. lanata* sensu stricto. The apparent distinction between these two species breaks down, however, because the degree of upper leaf pubescence and style length forms a continuum. Therefore *C. lanata* should include *C. rosei*.

CLETHRA OLEOIDES AND *CLETHRA GELIDA*

Clethra oleoides L. Wms. and *C. gelida* Standl. appear to be closely related. They are unique in having small leaves and peduncles that curve downward and are collected usually above 2,800 m elevation, in elfin forest. I can find only one good character to differentiate the two: the leaf underside texture of *C. gelida* is ferrugineous, whereas that of *C. oleoides* is rough and glandular but not pubescent. *Clethra oleoides* occurs in Mexico and Guatemala, whereas *C. gelida* occurs in Costa Rica; presumably the present-day paucity of suitable habitat between their ranges has resulted in the isolation of populations and consequent speciation.

THREE NEW SPECIES FROM MEXICO

Clethra breedlovei C. Hamilton, sp. nov. TYPE: Mexico. Guerrero: ENE of Puerto El Gallo, 2,700–2,850 m, 11 Nov. 1973 (fl), *Breedlove 36098* (holotype, MO-2243945; isotype, CAS).

Arbor ca. 10 m alta, dense atrorufo-setosa atque stellato-pubescens. Folia petiolis 1.3–1.8 cm longis, laminis 7–12 cm longis, 2.5–5.5 cm latis, supra brunneo-stellato-pubescentibus sulcis nerviorum mediorum dense brunneo-stellato-pubescentibus, infra dense pallido-tomentosis atque ferrugineo-stellato-pubescentibus, venis secundariis 12–15 infra porphyreo-stellato-pubescentibus. Inflorescentiae terminales paniculatae contractae, ramis 6–10, ramis maturis (5–)6–8 cm longis, bracteolis usque ad 6 mm longis. Flores pedicellis 3–4(–5) mm longis; sepala linearia, 4–5 mm longa; petala 5.5–6.5 mm longa; stamina filamentis 2.5 mm longis, antheris 1.5 mm longis; stylus usque ad 3 mm longus. Fructus non visi.

Tree ca. 10 m; young branchlets densely deep brown setose and stellate-pubescent. *Leaves* with petioles 1.3–1.8 cm long, densely deep brown setose and stellate-pubescent, terete; blade rigid, elliptic, the apex acute or mucronulate, the base cuneate to obtuse, the margin entire or obscurely denticulate, not revolute at base, 7–12 cm long, 2.5–5.5 cm wide, green-yellow and regularly brown stellate-pubescent above with midvein furrow densely brown stellate-pubescent, densely pale tomentose and red-brown stellate-pubescent below; secondary veins 12–15 pairs, not furrowed above, prominulous below, rusty stellate-pubescent below. *Inflorescences* terminal contracted panicles with 6–10 branches, the mature branches (5–)6–8 cm long; rachises densely deep brown setose and stellate-pubescent; bracteoles to 6 mm long, linear, caducous. *Flowers* with pedicels 3–4(–5) mm long; sepals 5, linear, 4–5 mm long, tomentose without; petals 5, entire or short-fringed, 5.5–6.5 mm long; stamens 10, the filaments 2.5 mm long, the anthers 1.5 mm long; ovary pale tomentose, the style to 3 mm long. *Fruit* not seen.

This species is probably related to *C. mexicana*, with which it shares similar stout dark brown inflorescence rachises. *Clethra mexicana*

leaf blades are obovate to oblong and essentially glabrous above, whereas *C. breedlovei* leaf blades are elliptic and pubescent above.

Clethra oaxacana C. Hamilton, sp. nov. TYPE: Mexico. Oaxaca: road between Teotitlán del Camino and Huatla de Jiménez, 35 mi. E of Teotitlán, 1,650 m, 22 Feb. 1979 (imm. fl), *Croat 48252* (holotype, MO-2981877).

Arbor ca. 10 m alta, dense rufo-stellato-tomentosa. Folia petiolis 1.5–2 cm longis, laminis 10–14 cm longis, 4.5–7.5 cm latis, indumento stellato, supra brunneo-setosis sulcis venarum dense brunneo-setosis, infra ferrugineo-setosis, venis secundariis 9–12 infra dense ferrugineo-tomentosis. Racemi 5–8 fasciculati terminales, racemis 6–10 cm longis, bracteolis 2 mm longis. Flores pedicellis 3–4 mm longis; sepala linearia, 4 mm longa; petala ca. 4 mm longa; stamina filamentis ca. 2 mm longis, antheris 1.2 mm longis. Fructus non visi.

Tree ca. 10 m; young branchlets densely red-brown stellate-tomentose. *Leaves* with petioles 1.5–2 cm long, densely brown stellate-pubescent, terrete; blade subchartaceous, elliptic to obovate, the apex acute to cuspidate, the base obtuse to truncate, the margin denticulate, not revolute at base, 10–14 cm long, 4.5–7.5 cm wide, indumentum stellate, deep brown regularly setose above with vein furrows densely brown setose, red-brown setose below; secondary veins 9–12 pairs, shallow furrowed above, prominent below, densely red-brown tomentose below. *Inflorescences* terminal clusters of 5–8 racemes, the racemes 6–10 cm long; rachises densely red-brown stellate-tomentose; bracteoles 2 mm long, tomentose, linear, caducous. *Flowers* with pedicels 3–4 mm long; sepals 5, linear, 4 mm long, densely tomentose without; petals 5, fringed, ca. 4 mm long; stamens 10, the filaments ca. 2 mm long, the anthers 1.2 mm long; ovary velutinous. *Fruit* not seen.

This species appears related to *C. alexandri* Griseb., a Jamaican species with long (ca. 10 mm) bracteoles and larger flowers. *Clethra oaxacana* is related also to *C. michoacana* C. Hamilton (see following species description).

Clethra michoacana C. Hamilton, sp. nov. TYPE: Mexico. Michoacán: near San José Lagunillas, pine woods, 8,000 ft., 9 Sept. 1967 (imm. fl), *Oliver et al. 941* (holotype, MO-3099951; isotype, BM).

Arbor usque ad 15 m alta, dense ferrugineo-stellato-tomentosa. Folia petiolis 2.5–4 cm longis, laminis 15–18 cm longis, 8–10 cm latis, supra glabris sulcis venarum rufo-stellato-tomentosis, infra pallido-incanis atque ferrugineo-stellato-tomentosis, venis secundariis 13–16 infra dense ferrugineo-stellato-tomentosis. Racemi 5–7 fasciculati terminales, racemis 7–12 cm longis, bracteolis 9–13 cm longis. Flores pedicellis 1 mm longis, robustis; sepala ovato-linearia, minimum 4 mm longa. Fructus non visi.

Tree to 15 m; young branchlets densely red-brown stellate-tomentose. *Leaves* with petioles 2.5–4 cm long, densely red-brown stellate-tomentose, terete; blade rigid, obovate, the apex obtuse, the base obtuse, the margin entire, not revolute at base, 15–18 cm long, 8–10 cm wide, green-brown and glabrous above with vein furrows red-brown stellate-tomentose, pale pannose and red-brown stellate-tomentose below; secondary veins 13–16 pairs, furrowed above, prominent below, densely red-brown stellate-tomentose below. *Inflorescences* terminal clusters of 5–7 racemes, the racemes 7–12 cm long; rachises densely red-brown stellate-tomentose; bracteoles 9–13 mm long, linear, persistent in flower. *Flowers* with pedicels 1 mm long, robust; sepals 5, ovate-linear, at least 4 mm long, red-brown tomentose without; petals 5; stamens 10; ovary velutinous. *Fruit* not seen.

This species differs from the related *C. oaxacana* C. Hamilton in having more secondary veins, lacking setae on the upper leaf surface, and having longer, more persistent bracteoles. *Clethra michoacana* differs from the Jamaican *C. alexandri* Griseb. in having longer leaf blades (15–18 cm versus 8–12 cm) and more secondary veins (13–16 versus 8–12).

A New Species from Nicaragua

Sleumer (1967) cited only one Nicaraguan specimen in his entire treatment; intensive collecting since then has provided much more material, including a new species related to *C. lanata*.

Clethra nicaraguensis C. Hamilton, sp. nov. TYPE: Nicaragua. Jinotega: Carretera Matagalpa–Jinotega, Km 133–134, 1,400–1,480 m, 24 Feb. 1979 (fl), *Grijalva & Araquistain 166* (holotype, MO-3103450; isotypes, BM, CR, HNMN, MBM, MEXU, PMA, TEX, U, US, VEN, XAL).

Arbor 3–10 m alta, atrorufo-velutina. Folia petiolis (1–)1.5–2 cm longis, laminis 8–13 cm longis, 3.5–6 cm latis, supra glabris sulcis venarum sparse stellato-pilosis, infra rufo-lanatis atque stellato-pilosis, venis secundariis (9–)10–12(–14) infra atroferrugineo-villosis.

Racemi 4–12 fasciculati terminales et saepe racemis solitariis in axillis foliorum dispositis, racemis maturis 13–22 cm longis, bracteolis 3–5(–6) mm longis. Flores pedicellis 2–4(–5) mm longis; sepala ovato-linearia, 4 mm longa; petala 4 mm longa; stamina filamentis 2 mm longis, antheris 1 mm longis; stylus usque ad 2.5 mm longus. Fructus 4 mm longi, 4 mm diam.

Tree 3–10 m; young branchlets densely deep red-brown velutinous. *Leaves* with petioles (1–)1.5–2 cm long, densely deep rusty velutinous, often flattened above; blade coriaceous, obovate, the apex obtuse to subacute, the base cuneate, the margin entire or rarely denticulate near apex, revolute at base, 8–13 cm long, 3.5–6 cm wide, dull brown and glabrous above with vein furrows sparsely stellate-pubescent, pale red-brown woolly and stellate-pubescent below; secondary veins (9–)10–12(–14) pairs, furrowed above, prominent below, deep rusty villous below. *Inflorescences* terminal clusters of 4–12 racemes, often also with axillary racemes in distal 3–4 nodes, the mature racemes 13–22 cm long; rachises densely deep rusty velutinous; bracteoles 3–5(–6) mm long, linear, caducous. *Flowers* with pedicels 2–4(–5) mm long; sepals 5, ovate-linear, 4 mm long, tomentose within and without; petals 5, fringed, 4 mm long; stamens 10, the filaments 2 mm long, the anthers 1 mm long; ovary velutinous, the style to 2.5 mm long. *Fruit* a 3-lobed loculicidal capsule, 4 mm long, 4 mm diam., 7 mm diam. after dehiscence.

Distribution. Endemic to Nicaragua, 1,200–1,600 m. Flowers mostly from December to March, and fruits mostly from April to June.

Additional specimens examined. NICARAGUA. JINOTEGA: Carretera Matagalpa–Jinotega, 1,400–1,500 m, 2 July 1980 (fl), *Moreno 1108* (MO); 20 Aug. 1980 (fr), *Moreno 1874* (MO); Cerro Zamaria, 1,450 m, 5 July 1975 (fl), *Atwood & Neill 97* (BM, MO); Volcán Yalí, 1,500–1,542 m, 9 Apr. 1981 (fr), *Moreno 7924* (BM, HNMN, MO); Montaña Cuspire, 1,500–1,539 m, 10 Apr. 1981 (fr), *Moreno 8029* (BM, HNMN, MO). MATAGALPA: Cerro El Picacho, 1,500 m, 11 Feb. 1965 (fl), *Williams et al. 29181* (MO); finca Sta. María de Ostuma, 10 km N of Matagalpa, 12 Aug. 1977 (fr), *Neill 2312* (MO); El Porvenir, 1,700 m, 11 Mar. 1967 (fl), *Molina 20514* (MO). RIVAS: Ometepe, NE of Volcán Concepción, 13 Mar. 1981 (fl), *Sandino 564* (BM, MO). ZELAYA: Cerro El Hormiguerro, 1,100–1,183 m, 15 Apr. 1979 (fr), *Pipoly 5173* (BM, CR, HNMN, MBM, MEXU, MO).

Clethra nicaraguensis is distinguished from *C. lanata,* probably its closest relative, by its deep rusty pubescence on the leaf blade undersides and rachises and by its smaller flowers and fruits. *Clethra nicaraguensis* superficially resembles *C. mexicana* in having a dark-pubescent, sturdy inflorescence but differs in having smaller fruit (4 mm versus 5–6 mm diam.), much less robust rachises, and shorter leaf blades (8–13 cm versus 10–16 cm long).

A NEW SPECIES FROM COSTA RICA

Clethra talamancana C. Hamilton, sp. nov. TYPE: Costa Rica. Cartago: SE slope of Cerro de la Muerta, Cordillera de Talamanca, along Interamerican Highway, 2,700 m, 23 May 1976 (fl), *Croat 35400* (holotype, MO-3099952; isotype, BM).

Arbor ca. 3 m alta, rufo-stellato-pubescens. Folia petiolis 1.3–2 cm longis, laminis (5–)6–10 cm longis, 2–4 cm latis, indumento stellato, supra pallido-puberulis sulcis venarum dense pubescentibus, infra pallido-incanis atque rufo-pubescentibus, venis secundariis 12–15 infra ferrugineo-pubescentibus. Inflorescentiae terminales paniculatae contractae, ramis ca. 5, ramis maturis 8–12 cm longis, bracteolis 2–3 mm longis. Flores pedicellis 3–4 mm longis; sepala linearia, 3–3.5 mm longa; petala 4 mm longa; stamina filamentis 1.2 mm longis, antheris 0.8 mm longis; stylus ca. 1.5 mm longus. Fructus non visi.

Tree ca. 3 m; young branchlets red-brown stellate-pubescent. *Leaves* with petioles 1.3–2 cm long, densely red-brown stellate-pubescent, terete; blade subcoriaceous, elliptic-obovate, the apex mucronate to acuminate, the base cuneate, the margin mucronate-denticulate throughout, not revolute at base, (5–)6–10 cm long, 2–4 cm wide, indumentum stellate, dull brown and regularly pale puberulent above with vein furrows more densely pubescent, pale pannose and red-brown pubescent below; secondary veins 12–15 pairs, shallowly furrowed above, prominulous below, red-brown pubescent below. *Inflorescences* terminal contracted panicles of ca. 5 branches, the mature branches 8–12 cm long; rachises red-brown pubescent; bracteoles 2–3 mm long, linear, caducous. *Flowers* with pedicels 3–4 mm long; sepals 5, linear, 3–3.5 mm long, puberulent without; petals 5, fringed, 4 mm long; stamens 10, the filaments 1.2 mm long, the anthers 0.8 mm long; ovary pubescent, the style ca. 1.5 mm long. *Fruit* not seen.

The dense red-brown pubescence, small leaves, and short sepals distinguish *C. talamancana* from other *Clethra* species. As more material is collected from high elevations in Costa Rica and Panama, perhaps additional new species will be found to shed light on the presently unknown

affinities of this and the following two species from Panama.

Two New Species from Panama

Clethra tutensis C. Hamilton, sp. nov. TYPE: Panama. Veraguas: Cerro Tute, ca. 10 km NW of Santa Fe, on ridgetop in cloud forest, over 1,000 m, 3 Aug. 1975 (fr), *Mori et al. 7574* (holotype, MO-3099953; isotypes, BM, MEXU, PMA).

Arbor ca. 7 m alta, brunneo-adpresso-setosa. Folia petiolis 0.5–1 cm longis, laminis 2.5–3.5(–4) cm longis, 1.4–2.2 cm latis, supra glabris sulcis venarum glabris, infra glabris, venis secundariis 7–9 infra rufo-adpresso-setosis. Racemi 5–10 fasciculati terminales, racemis maturis (6–)7–10(–11) cm longis, bracteolis non visis. Flores non visi. Fructus 4 mm longi, 4–5 mm diam.

Tree ca. 7 m; young branchlets brown appressed-setose. *Leaves* with petioles 0.5–1 cm long, brown appressed-setose, flattened above; blade subcoriaceous, elliptic to slightly obovate, the apex mucronate-acute, the base cuneate, the margin mucronate-denticulate throughout, not revolute at base, 2.5–3.5(–4) cm long, 1.4–2.2 cm wide, dark brown and glabrous above, pale brown and glabrous below; secondary veins 7–9, furrowed and glabrous above, prominent and red-brown appressed-setose below. *Inflorescences* terminal clusters of 5–10 racemes, the mature racemes (6–)7–10(–11) cm long; rachises red-brown puberulent; bracteoles not seen. *Flowers* not seen. *Fruit* a 3-lobed loculicidal capsule, 4 mm long, 4–5 mm diam., 6–7 mm diam. after dehiscence.

The small leaves, large fruit, and clustered inflorescences distinguish *C. tutensis* from all other species of *Clethra*; its affinities are unknown.

Clethra coloradensis C. Hamilton, sp. nov. TYPE: Panama. Chiriquí: Cerro Colorado, 50 km N of San Felix on continental divide, cloud forest, 1,200–1,500 m, 17 Aug. 1975 (fr), *Mori & Dressler 7768* (holotype, MO-3099954; isotypes, BM, MEXU, PMA).

Arbor 8–12 m alta, dense rufo-stellato-tomentosa. Folia petiolis 0.8–1.5 cm longis, laminis 4–6 cm longis, 2.5–4 cm latis, indumento stellato, supra puberulis glabrescentibus sulcis venarum dense puberulis, infra pallido-incanis atque ferrugineo-puberulis, venis secundariis 8–10 infra ferrugineo-puberulis. Racemi 6–8 fasciculati terminales, racemis maturis 5–8 cm longis, bracteolis 2.5–3 mm longis. Flores pedicellis 0.5–1 mm longis; sepala ovata, 3 mm longa; petala ca. 3 mm longa. Fructus 2–2.5 cm longi, 3 cm diam.

Tree 8–12 m; young branchlets densely red-brown stellate-tomentose. *Leaves* with petioles 0.8–1.5 cm long, densely red-brown stellate-tomentose, terete; blade rigid, obovate, the apex mucronulate-obtuse, the base cuneate, the margin entire, not revolute at base, 4–6 cm long, 2.5–4 cm wide, indumentum stellate, brown puberulent becoming glabrous above with vein furrows densely puberulent, pale pannose and red-brown puberulent below; secondary veins 8–10 pairs, shallow furrowed above, prominent below, red-brown puberulent below. *Inflorescences* terminal clusters of 6–8 racemes, the mature racemes 5–8 cm long; rachises red-brown tomentose; bracteoles 2.5–3 mm long, linear, caducous. *Flowers* with pedicels 0.5–1 mm long; sepals 5, ovate, 3 mm long, puberulent within and without; petals 5, fringed, ca. 3 mm long; stamens 10; ovary tomentose. *Fruit* a 3-lobed loculicidal capsule, 2–2.5 cm long, 3 mm diam., 4 mm diam. after dehiscence.

Additional specimens examined. PANAMA. CHIRIQUÍ: N of San Felix at Chiriquí-Bocas del Toro border, on Cerro Colorado copper mine road along continental divide 5,000–5,500 ft., 3 May 1975 (imm. fl), *Mori & Kallunki 5812* (MO, PMA).

The small, stellate-pubescent, and puberulent leaves, relatively short racemes, minute pedicels, and small fruit distinguish *C. coloradensis* from all other neotropical species of *Clethra*; its affinities are unknown.

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BUMELIA RECLINATA VAR. *AUSTROFLORIDENSIS* (SAPOTACEAE), A NEW VARIETY FROM SOUTH FLORIDA, U.S.A.[1]

R. DAVID WHETSTONE[2]

ABSTRACT

Taxonomic studies in the Saptotaceae of the Southeastern United States support the recognition of three infraspecific taxa of *Bumelia reclinata* (Michaux) Ventenat: var. *reclinata,* var. *rufotomentosa* (Small) Cronquist, and var. *austrofloridensis* Whetstone, var. nov. A key to the infraspecific taxa and distribution map are included.

Bumelia reclinata is endemic to the outer Coastal Plain of the Southeastern United States. Members of this genus have been taxonomically revised by Asa Gray (1886), J. K. Small (1900), and R. B. Clark (1942) who primarily studied the North American taxa and by Arthur Cronquist (1945) who studied the New World representatives.

Bumelia reclinata (Michaux) Ventenat comprises three varieities, i.e., var. *reclinata,* var. *rufotomentosa* (Small) Cronquist, and var. *austrofloridensis* Whetstone. Of the more recent treatments, Clark (1942) recognized *B. rufotomentosa* and *B. reclinata* whereas Cronquist (1945) considered the two taxa as conspecific and relegated *B. rufotomentosa* to varietal status under the latter taxon. My conclusions are most similar to those of Cronquist but recognize the existence of a third variety that was overlooked by previous students (e.g., Cronquist, Clark, and Small who studied several specimens of var. *austrofloridensis*), perhaps due to the paucity of material available at that time. Those specimens studied by Small, Cronquist, and Clark were considered to belong to var. *reclinata.* The primary bases for my conclusions are close examination of almost 3,000 exsiccatae of *Bumelia* and field observations on all U.S. species.

Individuals of *B. reclinata* from the vicinity of Long Pine Key in the Florida Everglades are consistently and clearly separable from other taxa of the species by the following suite of character states:

a. leaves persistently tawny-pubescent across the abaxial surface of the lamina;
b. twigs essentially glabrous or glabrate;
c. pedicels pubescent;
d. inner and outer sepals pubescent;
e. ovary pubescent;
f. fruits basally pubescent; and
g. fruits not exceeding 9 mm in length.

(See Table 1 for summary of key characteristics of all varieties.) Variety *austrofloridensis* is common in hammocks and slash pine flatwoods in the Florida Everglades. The known range extends from Long Pine Key to hammocks immediately east of the Key. It is noteworthy that all known localities are within the Everglades National Park. As far as I have determined, no other members of *B. reclinata* are sympatric although *B. celastrina* H.B.K. and *B. salicifolia* (L.) Swartz occur on the Key (Fig. 1). Due to the limited geographic distribution and rarity of this taxon, I offer the name "Everglades Buckthorn" for those individuals and governmental agencies dealing with threatened and endangered species.

KEY TO THE INFRASPECIFIC TAXA OF *B. RECLINATA*

1a. Abaxial surfaces of fully expanded leaves persistently pubescent across the lamina; twigs essentially glabrous; pedicels, inner and outer sepals strigose ..... var. *austrofloridensis*

1b. Abaxial surfaces of fully expanded leaves glabrous or pubescent only along the midrib; twigs sparsely strigose (glabrate) to densely pubescent; pedicels, inner and outer sepals glabrous to densely strigose.

[1] The author gratefully acknowledges the loan of specimens from the herbaria cited herein (acronyms are from Holmgren et al., 1981, except "JSU," vide Whetstone, 1983). In addition, support for this study was provided by a grant from the Faculty Research Committee of Jacksonville State University to assist with field work on the Nearctic *Bumelia.* All conclusions and facts presented are those perceived by the author. This paper is an outgrowth of a treatment of the Sapotaceae for the "Vascular Flora of the Southeastern United States" (L. S. Radford, executive editor, in prep. Univ. of North Carolina Press, Chapel Hill). Descriptions generally follow the preferred format set forth by the editorial committee.

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TABLE 1. Comparison of key characteristics within varieties of *Bumelia reclinata*.

rufotomentosa	*reclinata*	*austrofloridensis*
Twigs densely strigose	Twigs glabrous	Twigs essentially glabrous
Leaf trichomes coppery	Leaf trichomes tawny	Leaf trichomes tawny
Leaf pubescence along abaxial surface of midvein	Leaf pubescence along abaxial surface of midvein	Leaf pubescence across the abaxial surface
Outer sepals and pedicels densely pubescent	Outer sepals and pedicels glabrous	Outer sepals and pedicels pubescent
Ovaries densely strigose at anthesis	Ovaries sparsely strigose at anthesis	Ovaries densely strigose at anthesis
Mature fruits ca. 11 mm long (or more)	Mature fruits ca. 9 mm long (or less)	Mature fruits ca. 9 mm long (or less)

2a. Leaves coppery pubescent on the petioles and along the abaxial surface of the midvein; twigs densely strigose; pedicels, inner and outer sepals densely pubescent ..... var. *rufotomentosa*

2b. Leaves rufous to tawny-pubescent (whitish) on the petioles and abaxial surface of the midvein (glabrate); twigs sparsely strigose to glabrous; pedicels and outer sepals glabrous, inner sepals glabrous to pubescent ..... var. *reclinata*

Bumelia reclinata (Michaux) Ventenat var. **austrofloridensis** Whetstone, var. nov. TYPE: United States. Florida: Dade County, Long

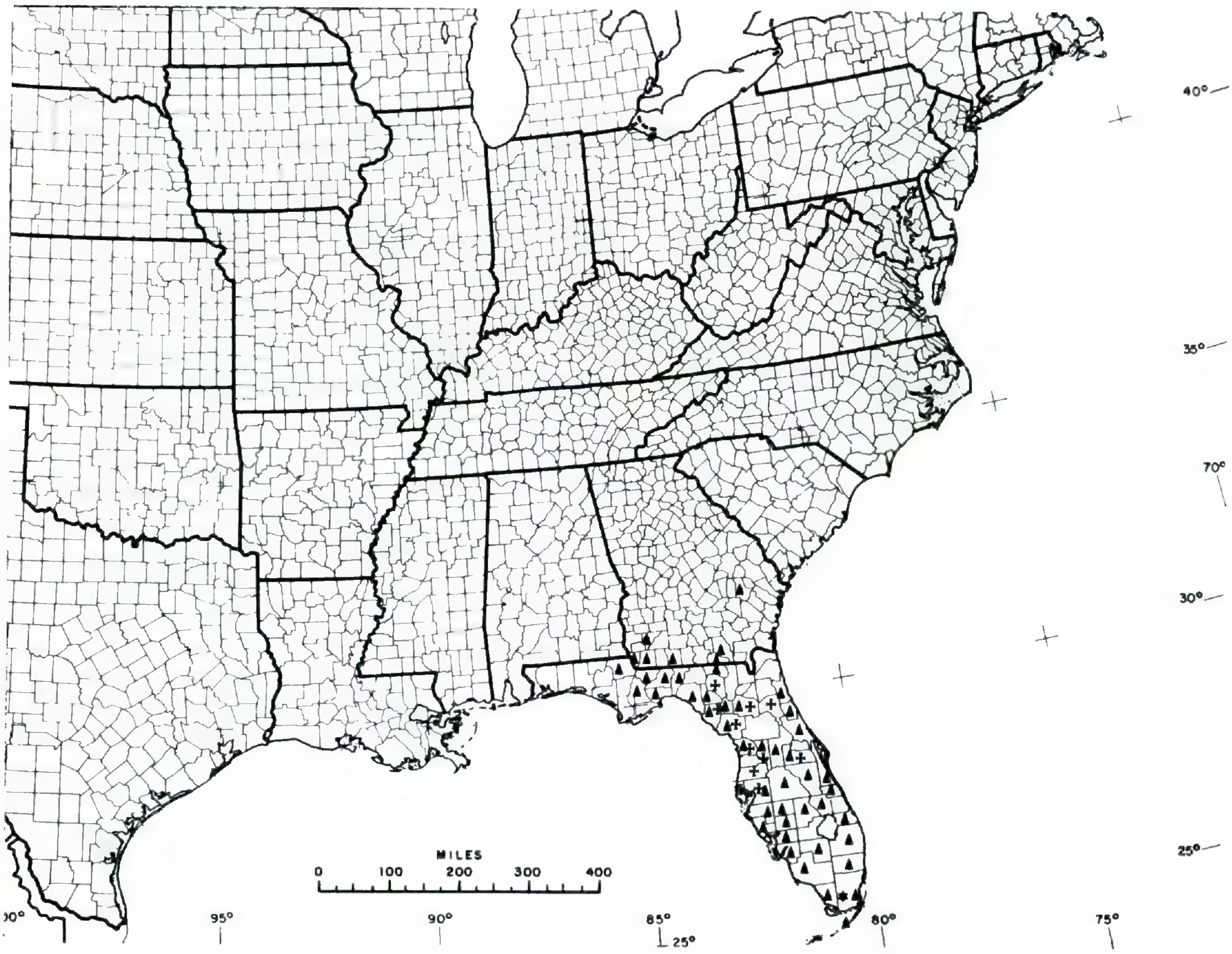
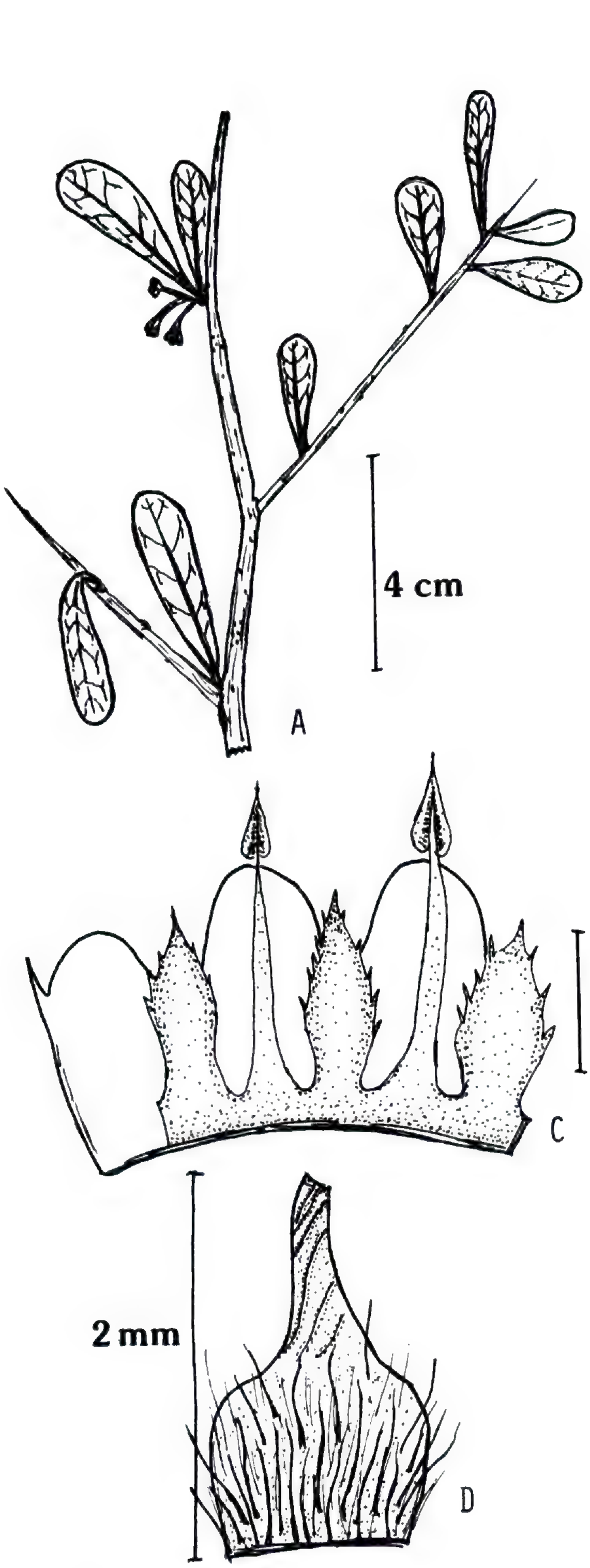


FIGURE 1. Map of the documented distribution of *Bumelia reclinata*. Triangle = var. *reclinata*; cross = var. *rufotomentosa*; and star = var. *austrofloridensis*.



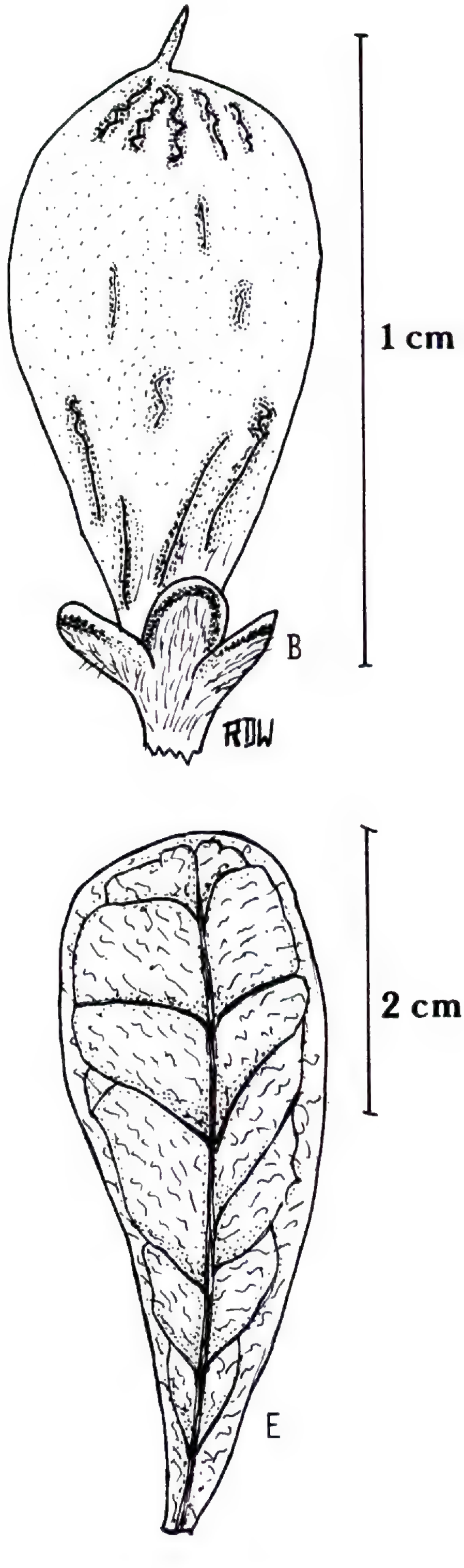


FIGURE 2. *Bumelia reclinata* var. *austrofloridensis*—A. Branch.—B. Fruit.—C. Adaxial view of androecium and corolla.—D. Gynoecium at anthesis.—E. Leaf details (blade).

Pine Key in the Everglades National Park, recently burned glade; over oolite. Abundant shrub, to ca. 1.5 m (isotypes collected from the same individual as holotype). 7 July 1984, *Whetstone 14459* (holotype, JSU 23555; isotypes, to be distributed to A, FLAS, FSU, MO, NCU, USF, VDB). Everglades Buckthorn. FIGURE 2.

Varietas nova *B. reclinata* optime distinguitur lobis calycis strigosis, ramunculo sparse strigoso ad glabrescens, ovario strigoso, et foliaris pubens persistens.

Small thorny shrubs. Twigs strigose, armed with thorns and knobby protuberances, essentially glabrous. Leaves evergreen, alternate to fascicled, oblanceolate, 1–4 cm long, fully expanded leaves with tawny pubescence on the abaxial surface of the lamina, apices rounded to emarginate, margins entire and somewhat revolute, bases acuminate with attenuate lamina forming an adaxial channel; petioles 2.5–3 mm long, densely pubescent basally. Flowers borne in loose, axillary fascicles at leafy and defoliated nodes. Flowers ca. 2.8 mm long, calyx of 5 imbricate sepals, sepals ovate, ca. 2 mm long, densely pubescent abaxially; corolla 5-lobed, whitish, lobes flared above the tube and broadly ovate with lateral appendages, margins erose; stamens epipetalous, anther slightly exerted, staminodes petaloid; gynoecium ca. 1.5 mm long, ovary densely strigose, style and stigma glabrous; pedicels 4–5(–9) mm long, pubescent apically with rufous trichomes. Fruits obovoid, ca. 9 mm long (excluding the apiculate stylar remnant), slightly pubescent basally and occasionally apically. Seeds ovoid, light brown, ca. 7 mm long, scar basilateral with a smaller adjacent scar.

Specimens examined. UNITED STATES. FLORIDA: Dade Co., *Bessey 2* (A), *75* (A), *Craighead, s.n.* (FLAS 146613, 146614, 146617), *Godfrey et al. 63394* (FSU 86781, NCU 253411), *63460* (FSU 86487), *77025* (FSU 154085), *Hill & Harvey, III, 3215* (NCU 462019), *Korsakoff, s.n.* (FLAS 42452), *Rehder 898* (A), *Small & Carter 2912* (NY), *2986* (NY), *2988* (NY), *2988* (NY), *2988a* (NY), *Whetstone 14427* (JSU), *14470* (JSU), *14474* (JSU).

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FIVE NEW TAXA OF NEW WORLD MEMECYLEAE (MELASTOMATACEAE)[1]

THOMAS MORLEY[2]

ABSTRACT

Three new species and one subspecies of *Mouriri* are described, with one new species of *Votomita*. *Mouriri peruviana* and *Votomita pubescens* occur in northeast Peru, *Mouriri pranceana* is from the elevated regions of southeast Pará and north Mato Grosso, Brazil, and *M. viridicosta* is from French Guiana. Relations of the first three are clear but *M. viridicosta* has no close relatives and does not fit well in any of the existing sections of the genus. *Mouriri cearensis* subsp. *carajasica* is a distinct inland form of the species.

New species of the Memecyleae (Melastomataceae) from the New World tropics are still discovered occasionally, usually where little-collected regions are explored more intensively but sometimes as with *M. viridicosta* through continued collecting in a relatively well-known country like French Guiana. The tribe is known well enough by now so that new discoveries can usually be placed to genus, subgenus, and section with certainty, but sometimes an exception appears, and *M. viridicosta* is one of these. This species has no known close relatives and its sectional affinities are in doubt. The other three species present no real problems. *Mouriri peruviana* is a western relative of *M. nervosa*, a widespread species of Amazonia. *Mouriri pranceana* is a close relative of *M. huberi* recently discovered through explorations of the Serra do Cachimbo and nearby regions; the new species is most readily distinguished by its fruit. *Votomita pubescens* is a seventh species of that genus, from farther west than the other species; it is the only known member of the tribe in the New World with a pubescent lamina.

Mouriri peruviana Morley, sp. nov. TYPE: Peru. Dpto. Huánuco: Prov. Pachitea, Dtto. Honoria, Bosque Nacional de Iparia, Región de "bosque seco tropical" (sensu Tosi, 1960) a lo largo del Río Pachitea cerca del campamento Miel de Abeja (1 km arriba del pueblo de Tournavista o unos 20 km arriba de la confluencia con el Río Ucayali). En bosque alto en el caserio Miel de Abeja a 2 km del campamento de Iparía. Altura sobre el mar 300–400 m. Arbusto 4–6 m, flores blancas con sépalos de color amarillo palido. "Sachavaca Shahuinto." 23 June 1967, *Schunke V. 2077* (holotype, F; isotype, US). FIGURE 1.

Frutex vel arbor usque 15 m alta; folia 11–25 cm longa; calyx ovarium inferum includens 6–8.5 mm longus; calyx 1.5–1.8 mm findens et productens inter lobos sub anthesi, lobi 1.5–2.5 mm longi ab staminibus, 3.5–5 mm lati post anthesin; antherae 4.3–4.5 mm longae; distantia ab basi styli ad stamina 3.6–4.8 mm; loculi ovarii 5, late separati, ut videtur intra basim hypanthii; placentae parietales in quoque loculo; lobi fructus 9.5–14 mm diam.; semina 9–12 mm diam.

Shrub or tree to 15 m high; young twigs rounded-quadrangular, not winged. Petioles 2–4 mm long; blades coriaceous, intensely green or yellowish green, 11–25 cm long, 5.7–8.5 cm wide, oblong, oblong-elliptic, or oblong-ovate, abruptly acuminate at the apex, rounded to cordate at base with a notch 2–8 mm deep; midrib plane above, prominent below with a flattened lower surface and short wings; lateral nerves obscure to moderately prominent above and below when dry. Midrib xylem tubular; stomatal crypts Type III (see Morley, 1976), averaging in a leaf 42–52 μm diam., 23–28 μm high, 95–108 per mm^2 (extremes 31–71 μm diam., 20–32 μm high, 89–141 per mm^2); upper epidermis one cell thick, most of the cells with mucilaginous walls; hypodermis none; terminal sclereids stellate, the central bodies relatively large, round to rectangular, seldom short-branching, with several to many short usually sharp arms. Inflorescences at leafless nodes of twigs 3–7 mm diam., 1–4 per side, each usually branching near the base, forming a dense cluster, each 1–9-flowered, 4–12 mm long to base of far-

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thest pedicel measured along the axes and with 2–3 internodes in that length; bracts triangular to ovate-triangular, 1.6–2 mm long, 1.8 mm wide, mostly deciduous by anthesis or shortly after. True pedicels 5–10 mm long, to 13 mm in fruit; calyx including inferior ovary 6–8.5 mm long, cup-shaped, the 5 locules widely separated and appearing as if in the base of the hypanthium and bulging somewhat externally; apparent free hypanthium as measured from style base to stamen attachments 3.6–4.8 mm; sepals yellowish green to pale yellow, 1 mm long, 2 mm wide, triangular, 1.5–2.5 mm long when measured from stamen attachment, stretching and splitting apart a further distance of 1.5–1.8 mm at anthesis, the sepals then 3.5–5 mm wide. Petals white. Filaments 7–9 mm long; anthers 4–4.5 mm long; sporangia 4–4.4 mm long, dehiscing by apical pores; gland 0.7–0.9 mm long, 2.5–2.8 mm from apex of anther when measured from center of gland; cauda none. Placentae parietal-basal in each of the 5 locules, the ovules 5, borne on all sides of a short parietal-basal column, ca. 25 in all; style ca. 16–18 mm long. Fruit consisting of 3–5 subglobose lobes independently attached to the old hypanthium and calyx, the lobes sometimes contacting each other but not laterally fused, reddish orange, 9.5–14 mm diam., 1-seeded or rarely 2-seeded, each lobe developed from 1 locule of the ovary. Seeds brown, polished except for the large hilum, irregularly spheroid, 8.5–10.2 mm high, 9.8–12 mm wide, 6–8 mm thick, with a small rounded hump on the polished side and a larger one on the hilum side, the hilum occupying all of one side except for a broad extension of the polished surface which curves over and down on the hilum side for ¼–⅓ of the height of that side.

Paratypes. PERU. LORETO: open woods, Masisea, 275 m, (fr) 25 July 1929, *Killip & Smith 26845* (F, NY, US); Coronel Portillo, Bosque Nacional de von Humboldt, Km 86, Pucallpa-Tingo Maria road, 270 m, Arboretum and adjacent carretera de extración, 75°00′W, 8°40′S, (fr) 7 Aug. 1980, *Gentry & Salazar 29438* (US). SAN MARTÍN: high ground in forest SE of house, Don Diogenes del Aguila, E of Aguaytia between Pucallpa Road and Río Aguaytia, (defl, fr) 28 June 1960, *Mathias & Taylor 5006* (F); Prov. Mariscal Caceres, Dtto. Tocache Nuevo, high forest SE of airport of Tocache Nuevo, 400 m, (fr) 10 Jan. 1970, *Schunke V. 3685* (F, US); Rio de la Plata, 1 km abajo de Tocache (margen derecha del Río Huallaga), (fr) 29 July 1974, *Schunke V. 7879* (US); 12 km W of Tocache Nuevo, near Río Tocache, mature flatland forest on lateritic soil, 500 m, 76°32′W, 8°10′S, (buds) 13 Mar. 1979, *Gentry, Schunke V. & Aronson 25651* (US).

Distribution. High forest to open woods in central Peru in the departments of Loreto, San Martin, and Huanuco in the drainages of the Huallaga and Ucayali Rivers at elevations of 270 to 500 m.

Mouriri peruviana is very simlar to *M. nervosa,* differing from the latter mostly in the greater size of its parts. The leaves of *M. peruviana* are somewhat larger than those of *M. nervosa,* the pedicels are somewhat longer, the calyx including the inferior ovary is larger, the calyx lobes are longer as measured from the stamen attachment, the anthers are longer and with a different shape, the lobes of the fruit and the contained seeds are larger, and the seeds have a different shape.

Although most of these are differences of size, the new plants are considered to represent a species rather than a subspecific taxon of *M. nervosa* because of the gaps between the size-ranges of the calyx and ovary, anthers, fruit lobes, and seeds in the two taxa, and because differences of shape are also seen in the anthers and seeds. The geographic range is also very distinct. Previously I mistook the collection *Killip & Smith 26845* to be *M. nervosa.* When this plant is properly recognized as *M. peruviana* the nearest *M. nervosa* is about 1,000 km to the east.

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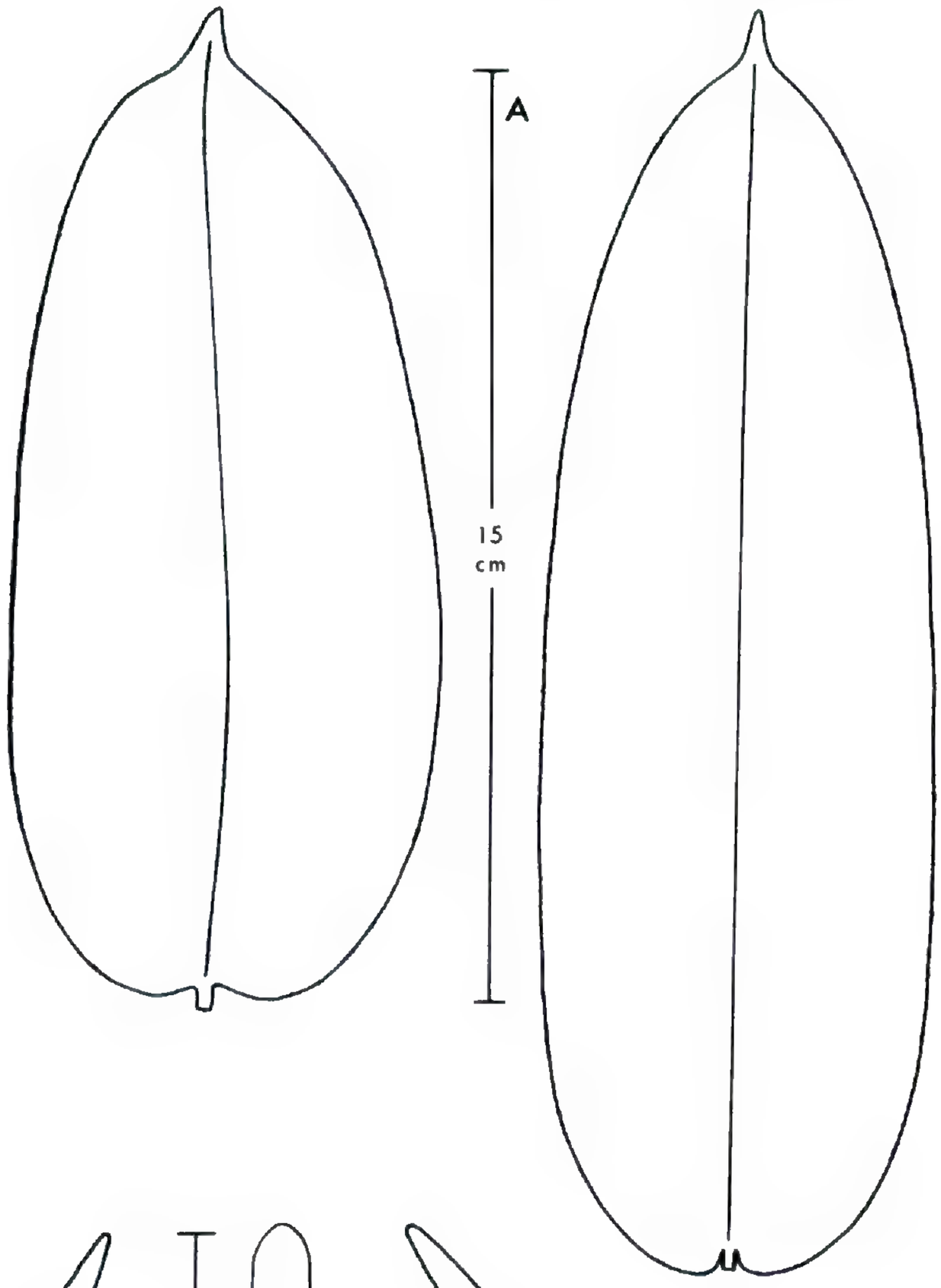
FIGURE 1. *Mouriri peruviana.*—A. Leaves.—B. Cleared portion of leaf blade showing terminal sclereids and veins (*Mathias & Taylor 5006*).—C. Cross section of leaf blade showing upper epidermis, sclereids, and stomatal crypts (*Killip & Smith 26845*).—D. Cross section of leaf midrib (*Killip & Smith 26845*).—E. Inflorescence (*Schunke 2077*).—F. Long section of flower, before anthesis (*Schunke 2077*).—G. Anther, shown cleared except for the sporangia (*Schnuke 2077*).—H. Fruit (*Schunke 7879*).—I, J. Seed (*Schunke 7879*).

FIGURE 2. *Mouriri pranceana.*—A. Leaves.—B. Cleared portion of leaf blade showing terminal sclereids and veins (*Prance et al. 25263*).—C. Cross section of leaf blade showing upper epidermis, sclereids, and stomatal crypts (*Prance et al. 25263*).—D. Cross section of leaf midrib (*Prance et al. 25263*).—E. Inflorescence (*Prance et al. 25263*).—F. Long section of flower, before anthesis (*Prance et al. 25263*).—G. Anther, shown cleared except for the sporangia (*Prance et al. 25263*).—H. Petal (*Prance et al. 25263*).—I. Fruit (*Pires 16105*).—J. Seed (*Pires 16105*).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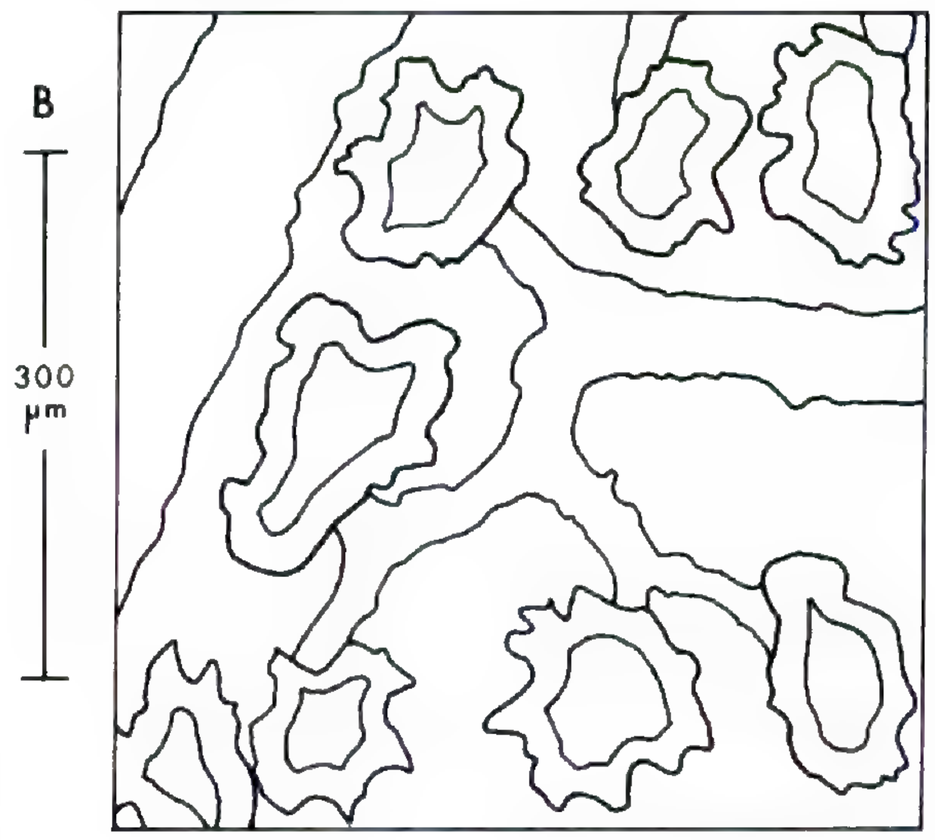
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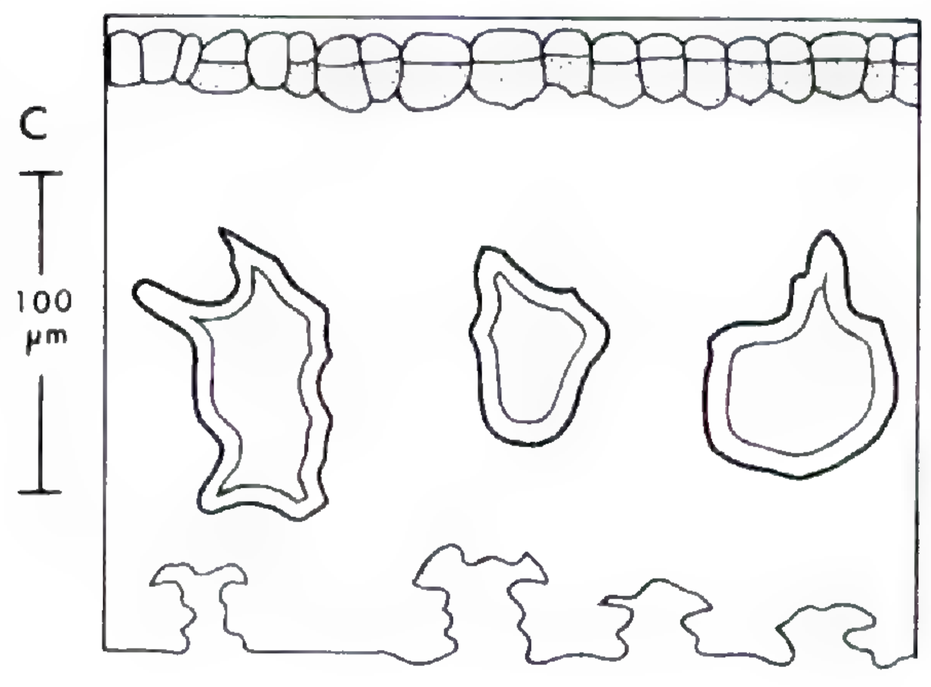
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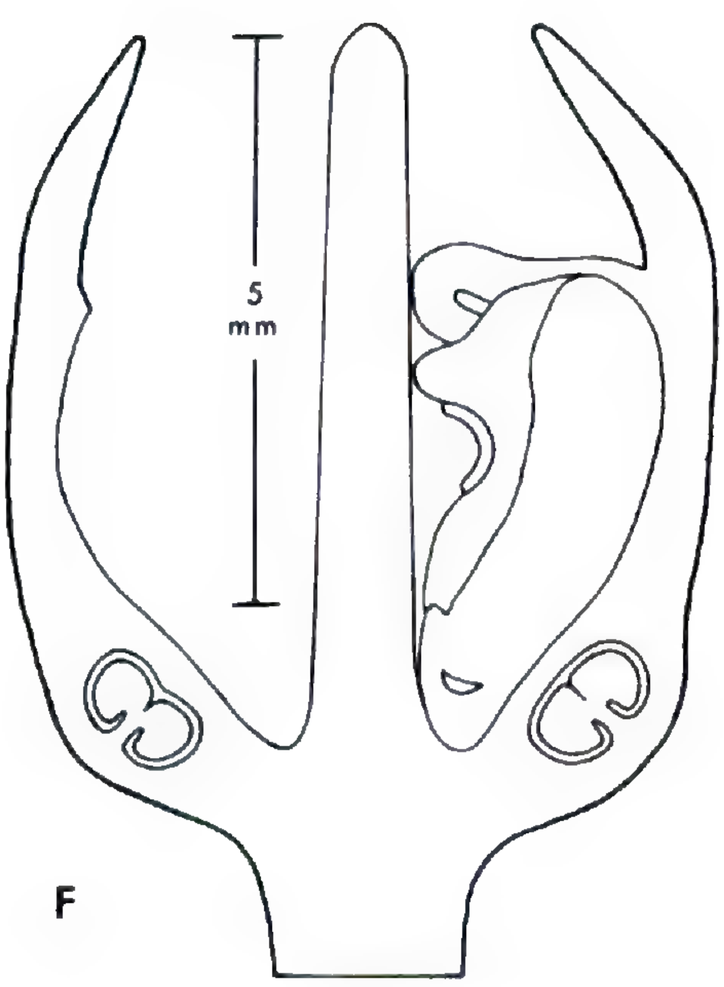
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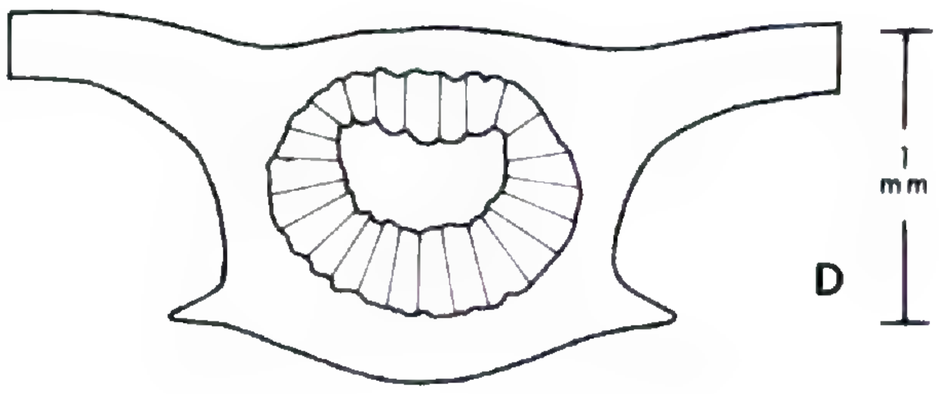
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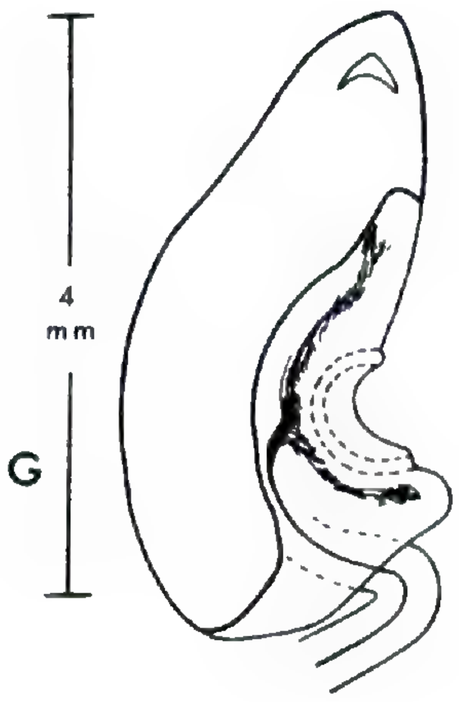
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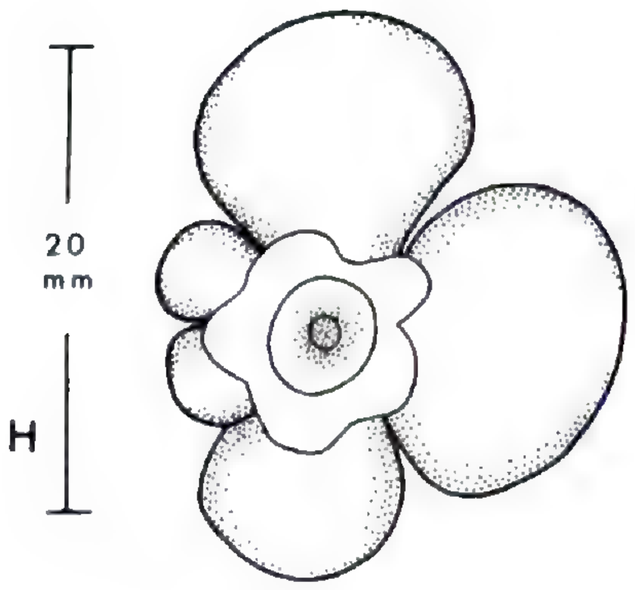
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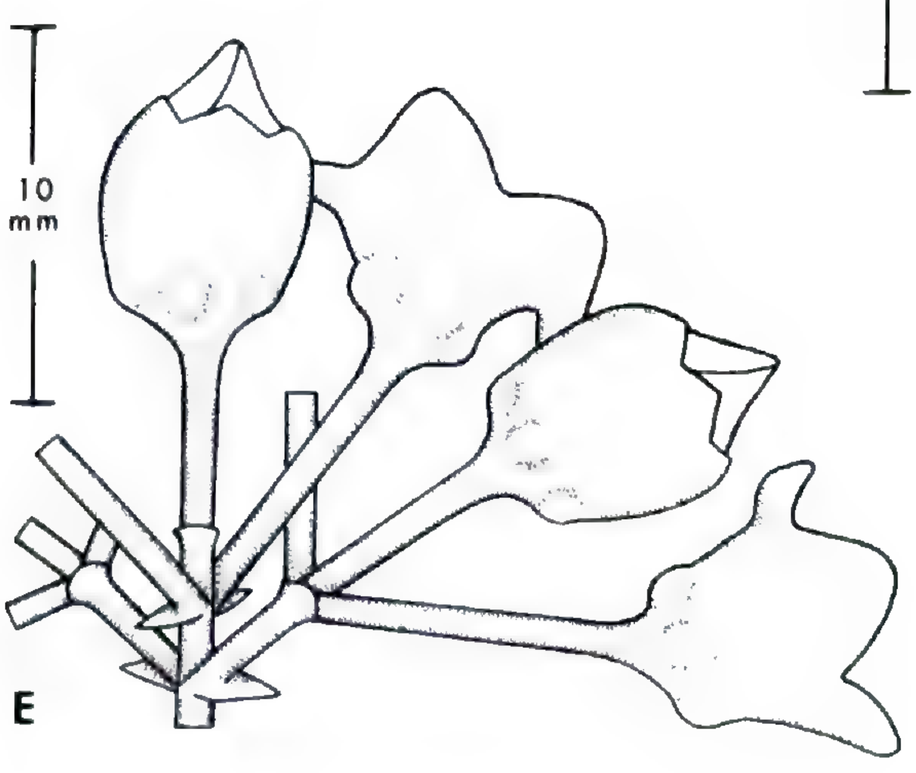
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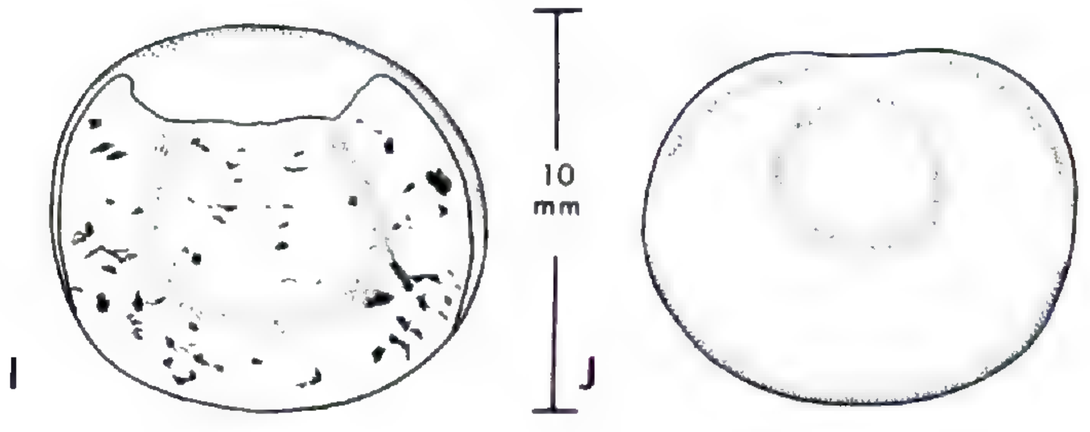
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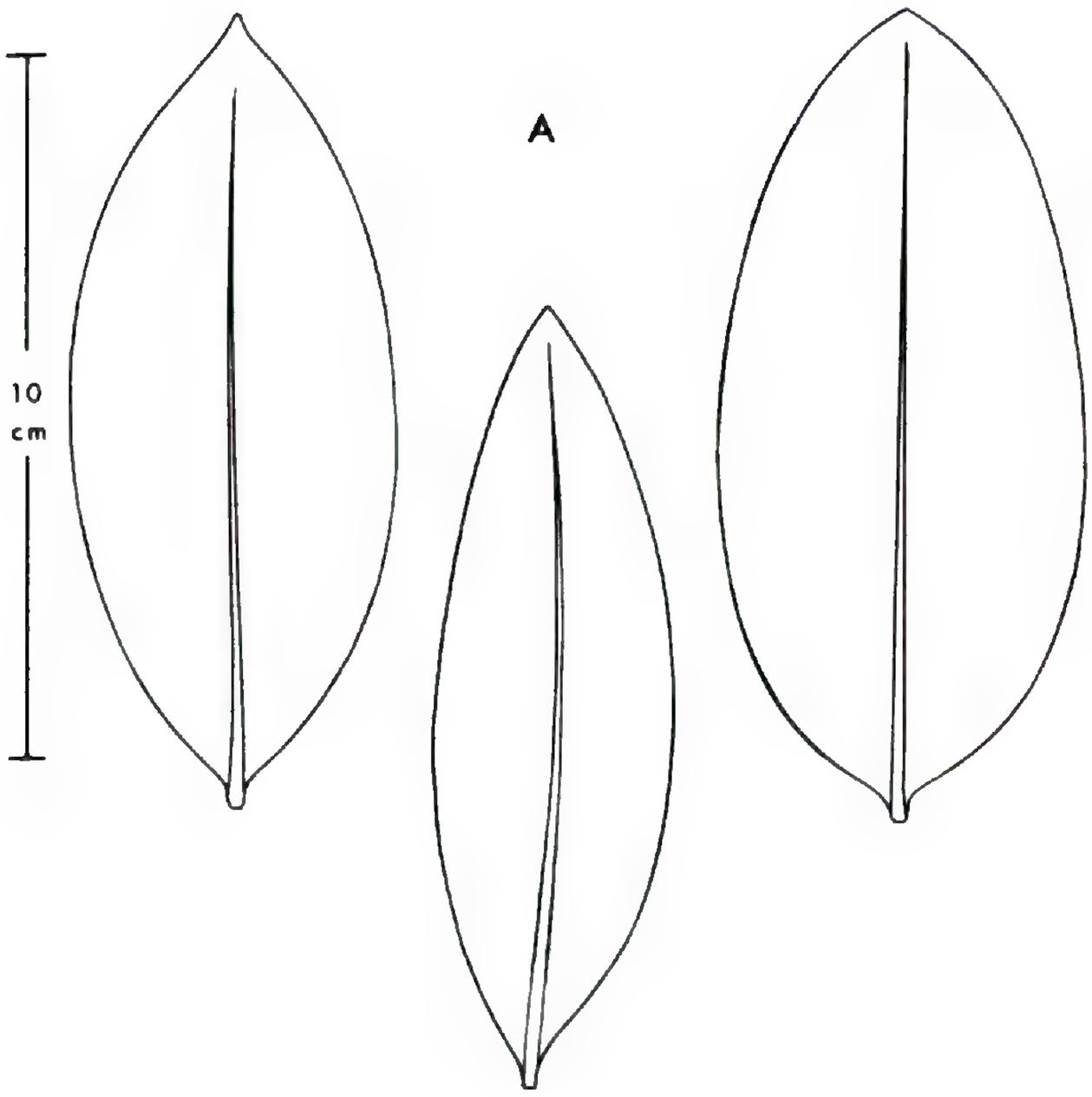
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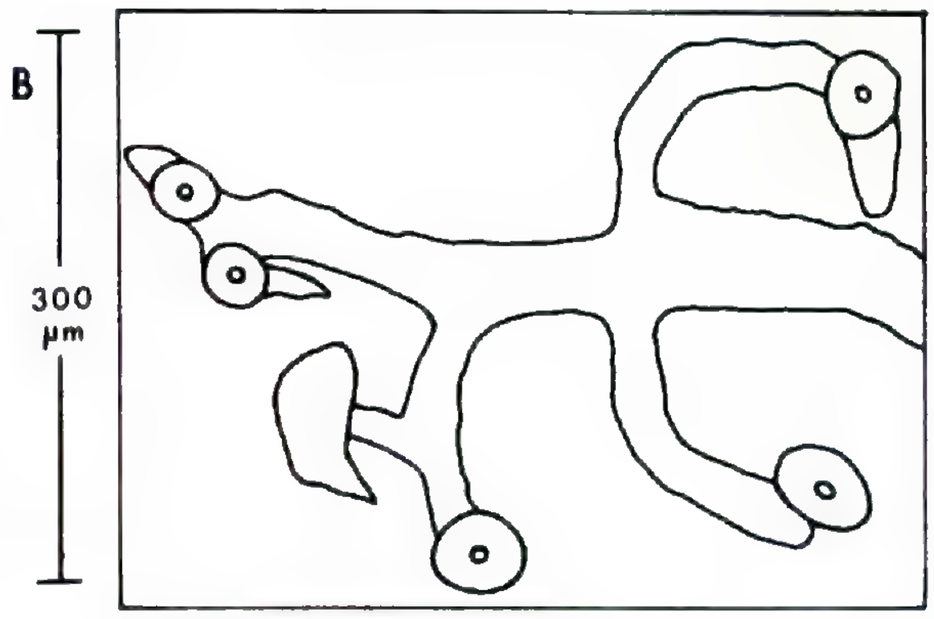
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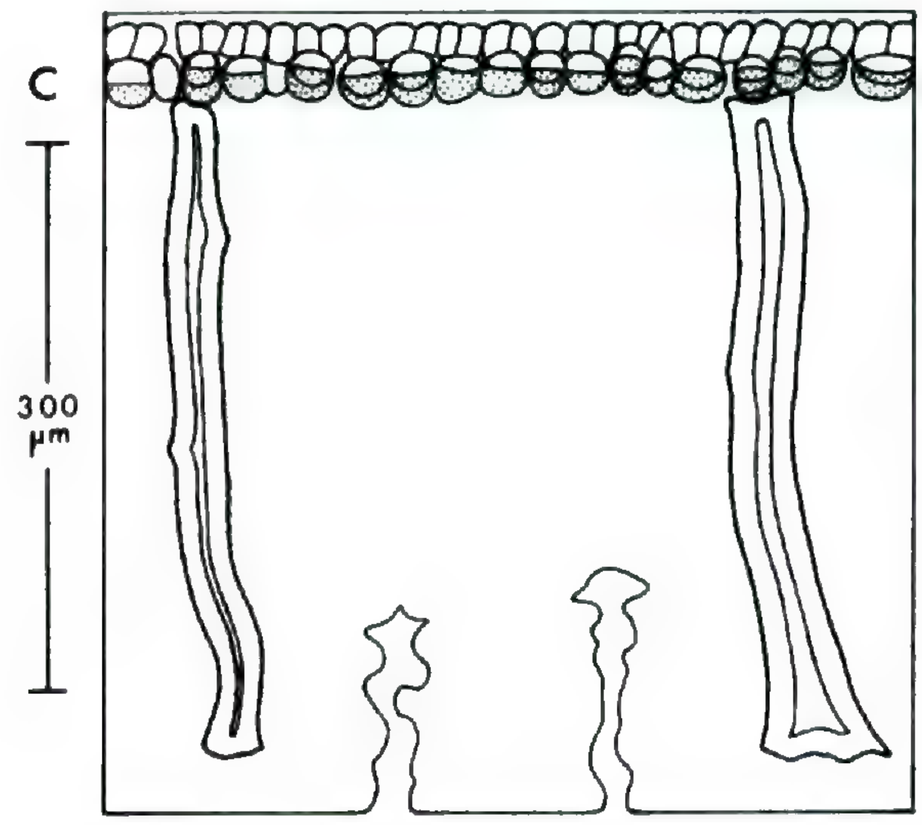
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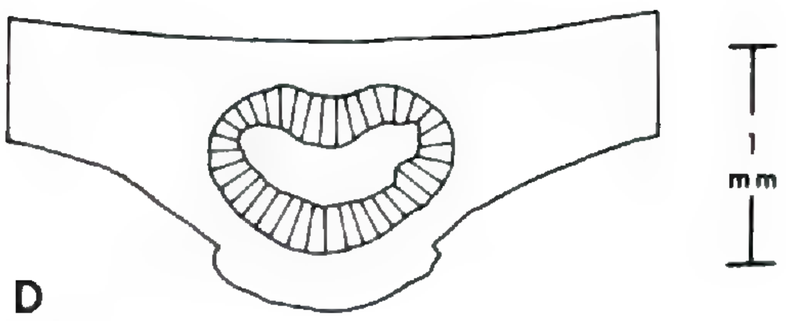
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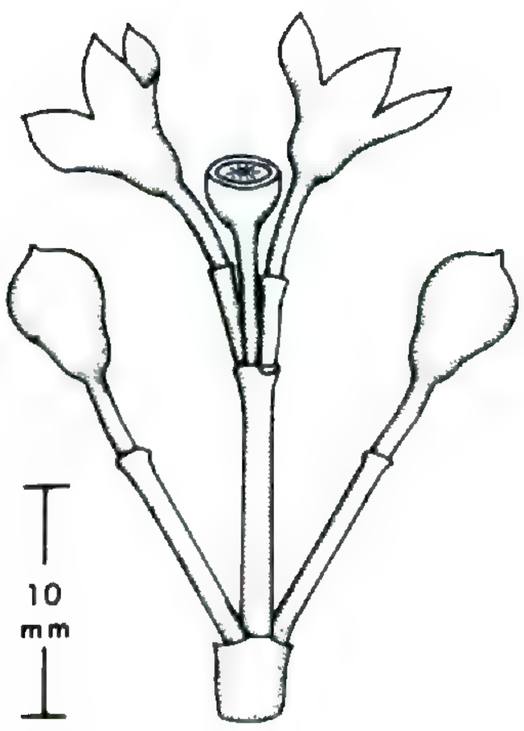
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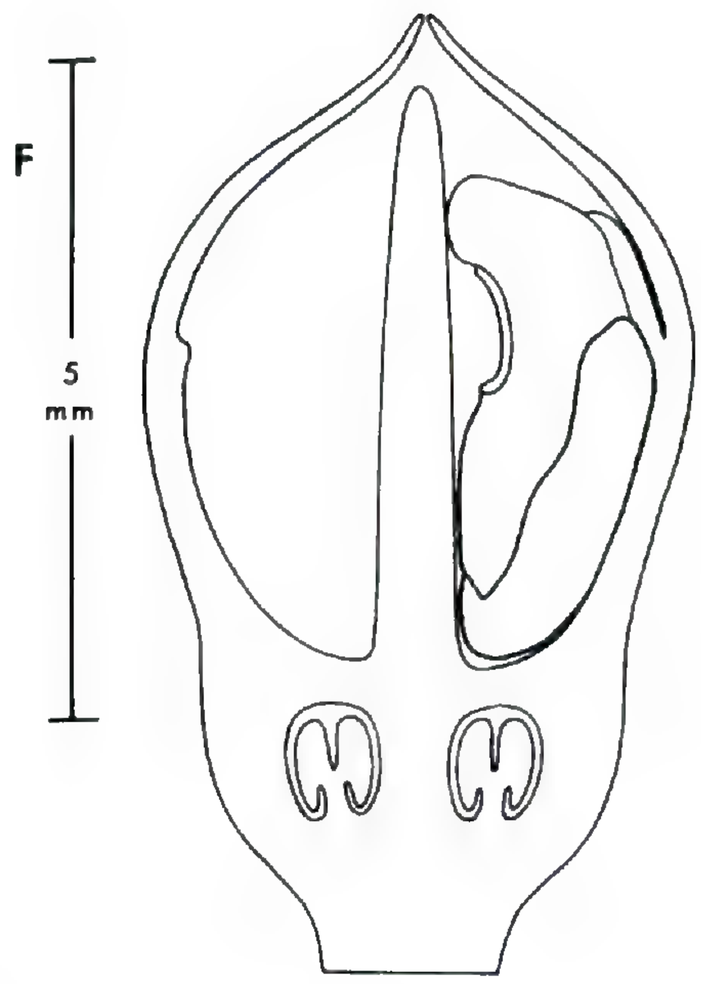
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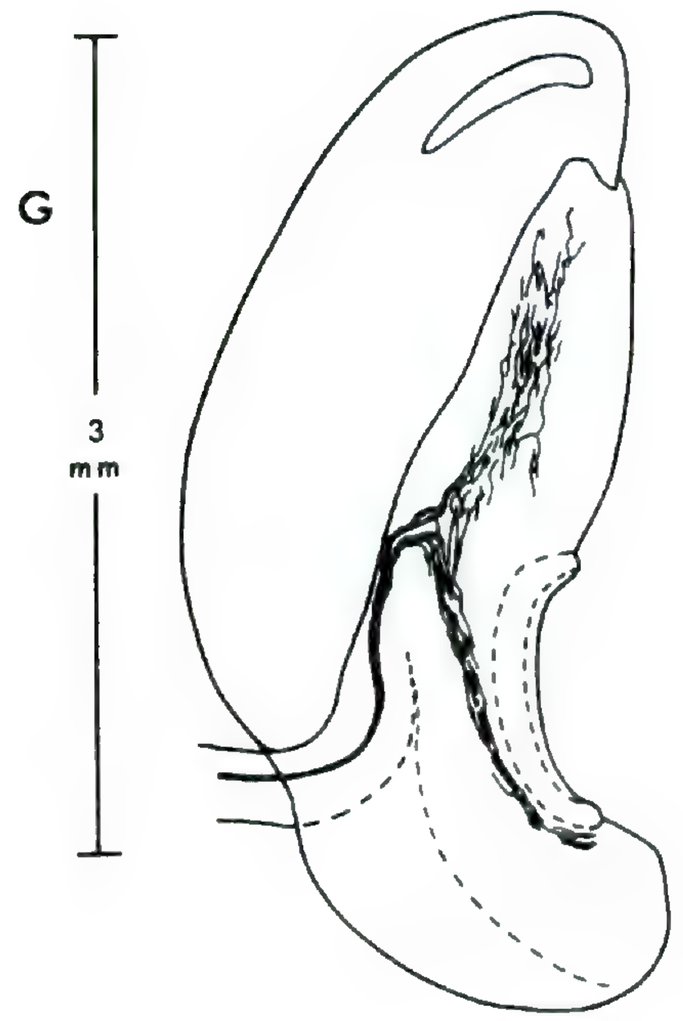
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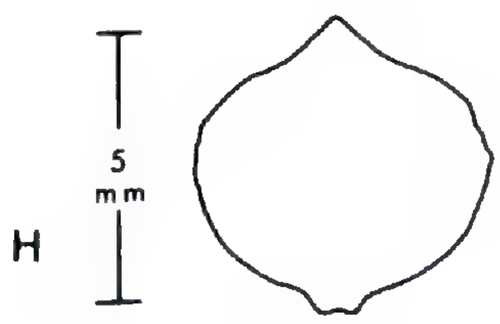
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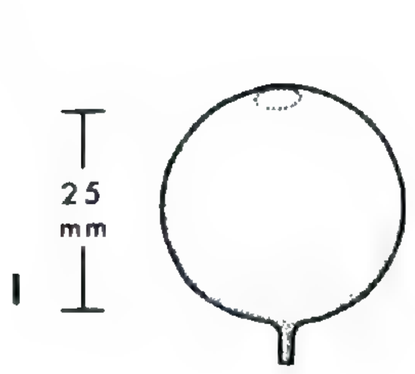
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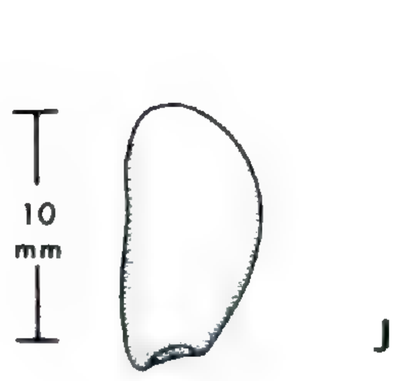
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Mouriri peruviana is also somewhat similar to *M. angustifolia,* a close relative of *M. nervosa* from the east-central border of Colombia. *Mouriri angustifolia* has still smaller leaves than *M. nervosa,* Type II crypts instead of Type III, shorter pedicels, smaller flowers and flower parts, and only three ovules per locule in the ovary.

The new species has sometimes been mistaken for *M. cauliflora* because the flowers of the latter are also rather large. However, *M. cauliflora* has a smooth lamina when dry, a prominently rounded midrib above with a groove on each side, and columnar foliar sclereids; the ovary locules of the ovary do not bulge outwardly in the flower, and the fruits and seeds are smaller. *Mouriri cauliflora* does occur in Peru, in Maynas and Requena Provinces of Loreto, but has not yet been found in the range of *M. peruviana.*

Mouriri pranceana Morley, sp. nov. TYPE: Brazil. Mato Grosso: Serra do Cachimbo, Cuiabá-Santarém highway, BR 163, Km 764, 15 km S of Mato Grosso/Pará border, 520 m. Disturbed campina forest. Tree 3 m; petals white. 12 Nov. 1977, *Prance, Silva, Berg, Henderson, Nelson, Balick, Bahia & dos Santos P 25263* (holotype, MG; isotype, US). FIGURE 2.

Frutex vel arbor usque 5 m alta; laminae apice acuto vel abrupte et brevissime acuto; superficies costae mediae plana; lobi calycis in alabastro connati, secedentes sub anthesi; hypanthium liberum circumscissum ca. 0.5 mm supra basim; ovarium 5-loculare; placentae basilares in quoque loculo, ovula circiter 4–5 undique circum quamque placentam genita; fructus subglobosus; cicatrix calycis 5.4–6.5 mm diam., laevis, non depressa, vix manifesta; hilum seminis 2.2–2.8 mm longum, 1.8–2 mm latum.

Shrub, or tree to 5 m high, glabrous except for the inflorescence; young twigs rounded, with 2 shallow channels on opposite sides. Petioles 3–5 mm long; blades coriaceous, with a dull shine when dry, 8.5–12 cm long, 3.3–5.2 cm wide, ovate-elliptic to elliptic or narrowly so or these slightly oblong, broadly to medium acute or abruptly very short acute at the apex, rounded to broadly or medium acute at base, the blade abruptly short-attenuate on the petiole; midrib flat above or occasionally with a slight narrow central groove, prominent below, low-rounded near the petiole, becoming 2-angled 1/6–1/4 of the way to the apex or very narrowly 2-winged; lateral nerves invisible to slightly visible above and below when dry. Midrib xylem tubular; stomatal crypts a highly modified Type II, averaging in a leaf 40–50 μm diam., 115–131 μm high, 69–120 per mm² (extremes 30–65 μm diam., 105–141 μm high, 54–135 per mm²); upper epidermis varying with the thickness of the leaf, in the thinner leaves being mostly 2 cells thick, rarely one, in thicker leaves 2 or 3 cells thick; conspicuous mucilaginous walls usually present in the cells contacting the palisade and also in the middle cells when the epidermis is 3 cells thick; hypodermis none; terminal sclereids columnar, narrow, sometimes with several short radiating branches at the epidermises. Inflorescences at leafless nodes of twigs to 7 mm thick or sometimes axillary, 1 per side, each 3–9-flowered, 14–23 mm long to base of farthest pedicel measured along the axes and with 2–3 internodes in that length; bracts early deciduous, unknown. Pedicels and at least the upper internodes of the inflorescence glabrous or very minutely puberulent. True pedicels 2.5–7 mm long; calyx including inferior ovary 6–8 mm long dry, to ca. 8.5 mm long fresh; calyx lobes fused to the apex of the flower in bud, splitting apart regularly at anthesis, each then ovate-triangular and acute, 3–3.8 mm long, 2.5–3 mm wide; free hypanthium 2.3–2.6 mm long measured to middle of the stamen attachment; calyx circumscissile a bit irregularly in the free hypanthium ca. 0.5 mm above the base after anthesis. Petals white, sometimes with a red line on the center of the exterior, broadly elliptic and acute, nearly sessile, ca. 5.4 mm long, 5.3 mm wide; mature filaments unknown; anthers yellow, 3.1–4 mm long; sporangia 2.4–3.3 mm long, dehiscing by apical slits; gland 0.8–1 mm long, 2.1–2.6 mm from apex of anther when measured from center of gland; cauda 1–1.5 mm long. Ovary 5-locular; placentae basal in each locule, the ovules borne on all sides of a short basal column, (3–)4–5 per placenta, 20–25 per ovary; mature style unknown. Fruit yellow and edible when ripe, tart when green, subglobose,

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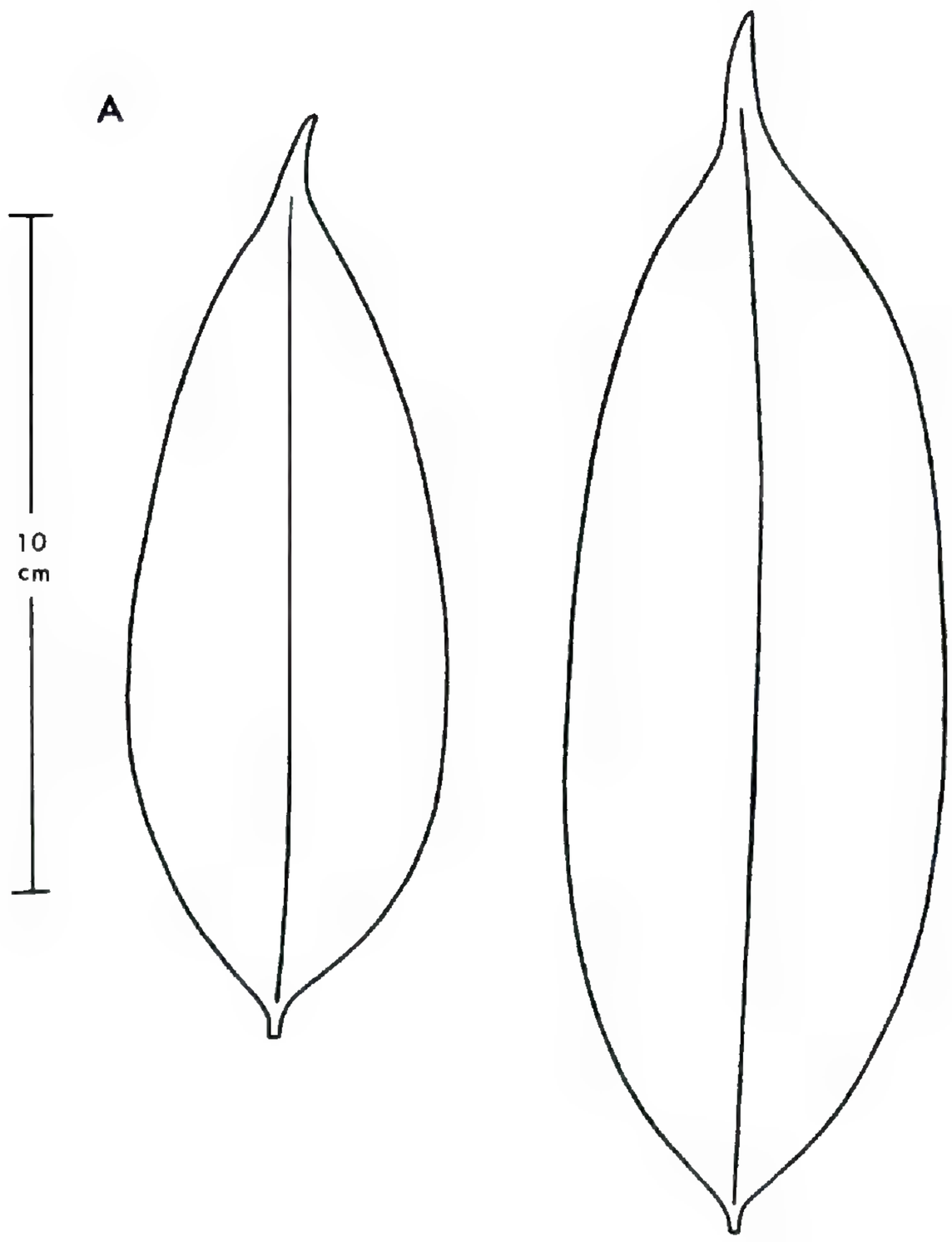
FIGURE 3. *Mouriri viridicosta* (*Lescure 834*).—A. Leaves.—B. Cleared portion of leaf blade showing terminal sclereids and veins.—C. Cross section of leaf blade showing upper epidermis and sclereids.—D. Cross section of leaf midrib.—E. Flower.—F. Long section of flower, before anthesis.—G. Inflorescence.—H. Fruit.—I. Seed.—J. Anther, shown cleared except for the sporangia.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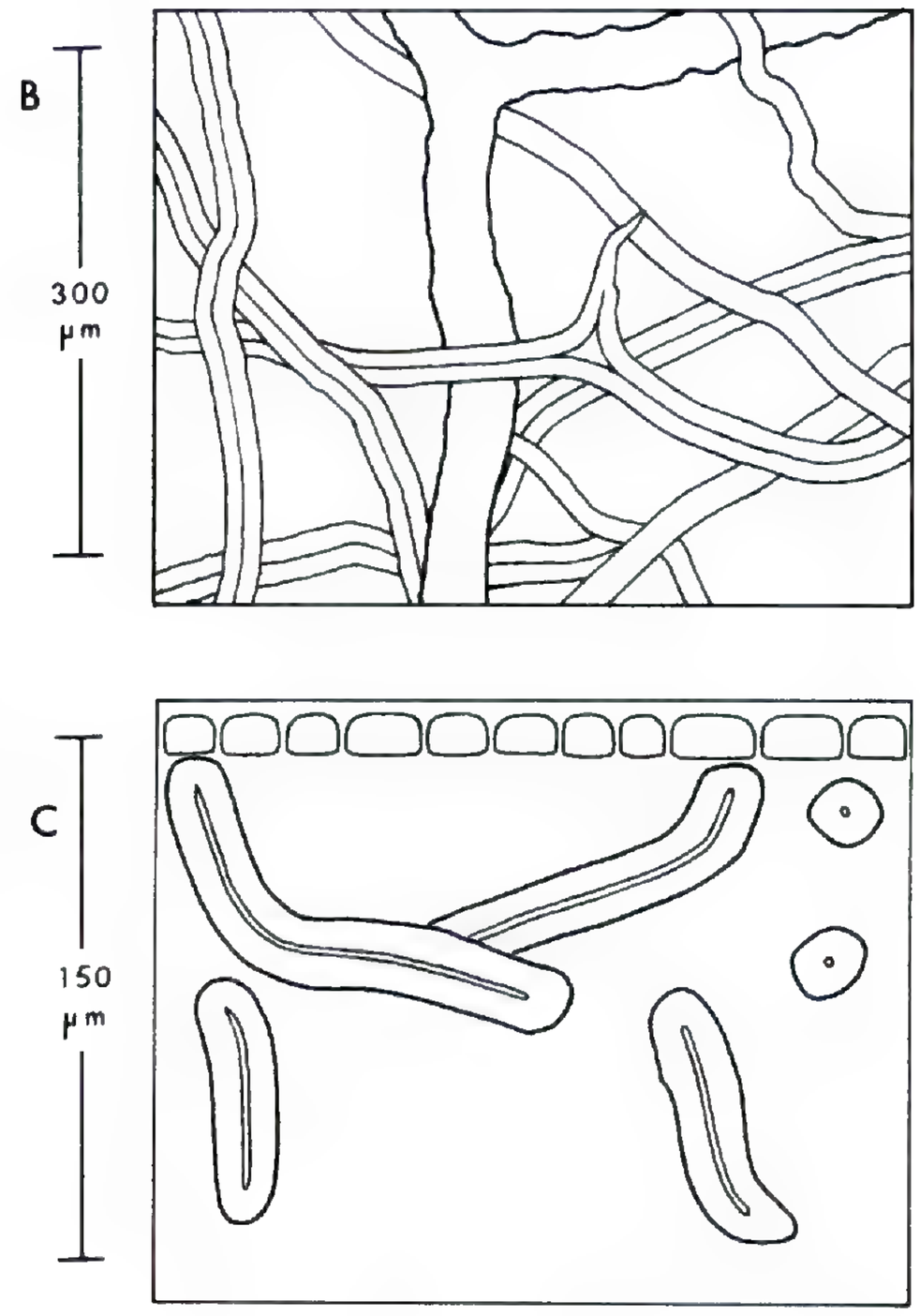
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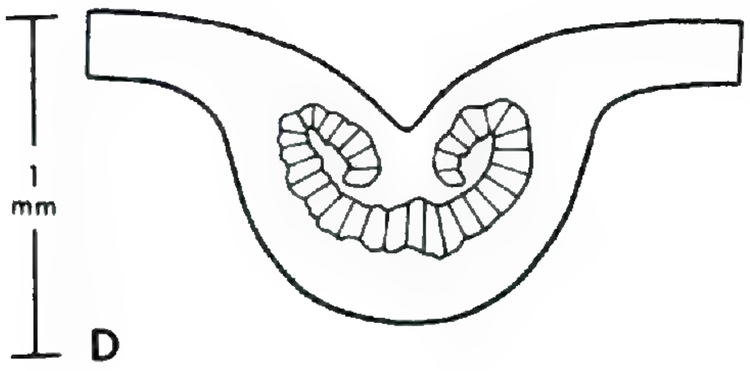
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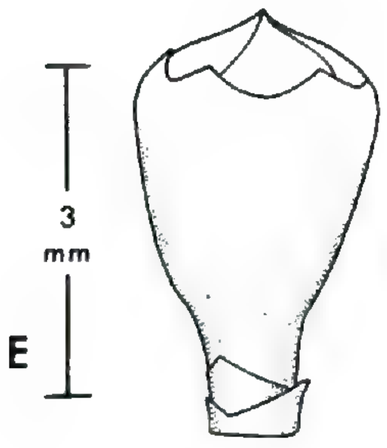
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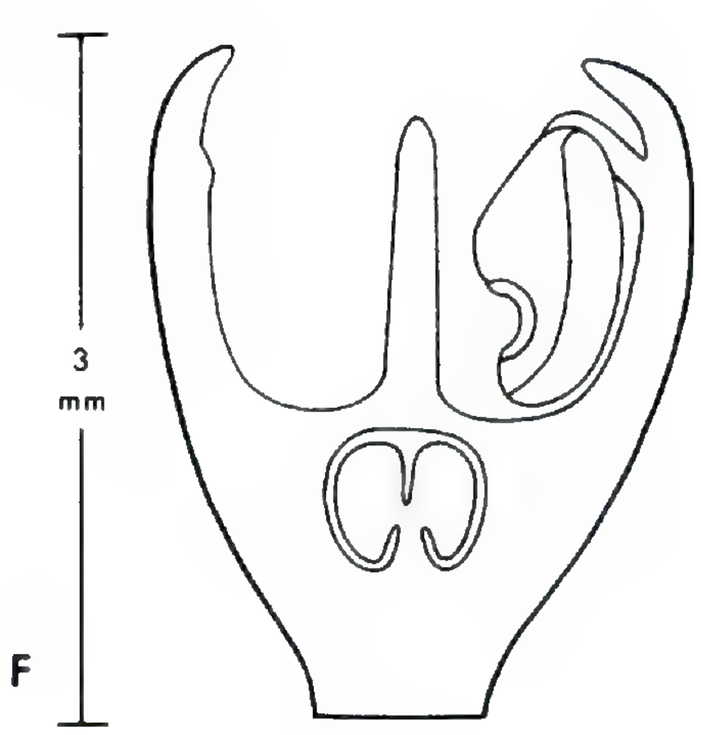
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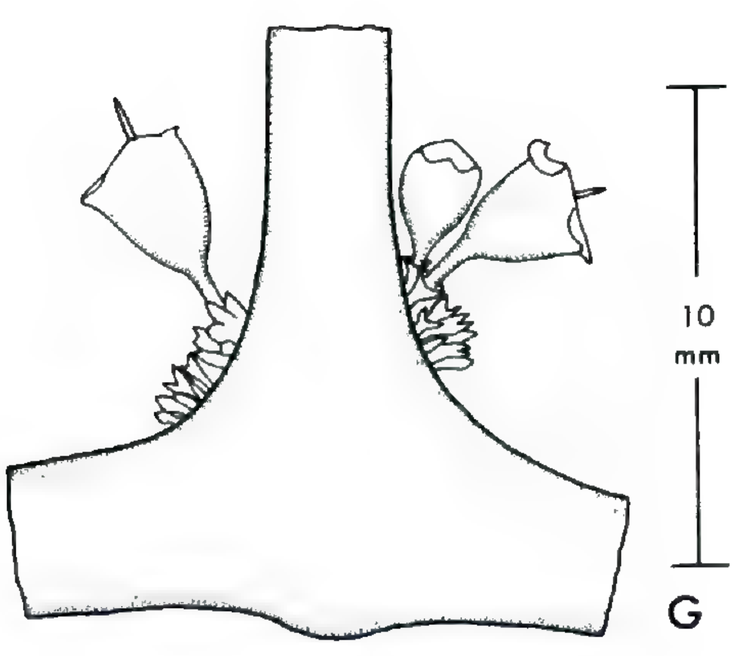
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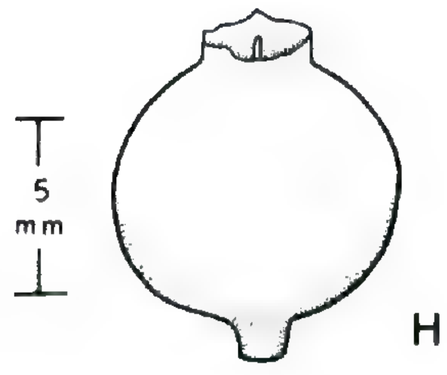
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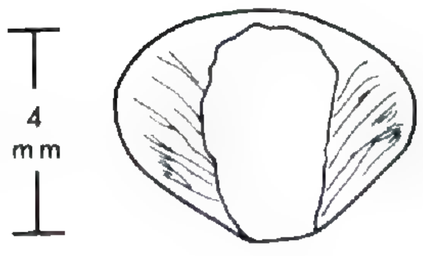
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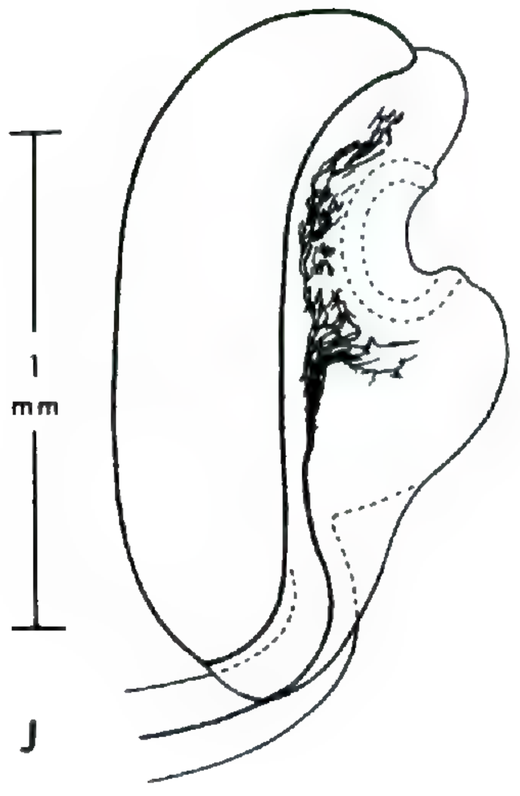
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estimated ca. 28 mm diam., with a smooth round calyx scar 5.4–6.5 mm diam. that is scarcely visible. Seeds 5 in the fruit examined, dark brown and polished, narrowly and irregularly ellipsoid, 12.8–12.9 mm long, 6.8–7.6 mm wide, 6.7–7.4 mm thick; hilum basal, angled slightly upward away from the center of the fruit, irregularly roundish in shape, 2.2–2.8 mm long, 1.8–2 mm wide.

Paratypes. BRAZIL. PARÁ: Serra do Cachimbo, BR 163, Cuiabá-Santarém highway, Cachoeira de Curuá, rocky terrain, 300 m, (bud, fr) 4 Nov. 1977, *Prance et al. P 24831* (US); Serra do Cachimbo, BR 163, Cuiabá-Santarém highway, Km 879, 2 km from Rio Curuá, low forest on terra firme, (fl) 11 Nov. 1977, *Prance et al. P 25189* (RB, US); alto Xingú, Fazenda Rio Dourado, R. Dourado afluente do R. Fresco, ca. 52°W, 8°S, mancha de savana pedrogosa no alto de morro, (fl, fr) 28 June 1978, *Pires 16105* (NY).

Distribution. Low forest to savanna to disturbed campina forest, often rocky, in southern Pará and adjacent Mato Grosso from the Serra do Cachimbo to the Xingu drainage at elevations from 300 to 520 m.

Mouriri pranceana clearly falls in the small section *Huberophytum,* owing largely to characters of the calyx and ovary. The calyx lobes are fused for their length in the bud and separate regularly at anthesis, the hypanthium is circumscissile post anthesis, and the placentation is typical for the section. Within *Huberophytum, M. pranceana* is distinct from *M. elliptica* and *M. cearensis* on the basis of habitat, habit, and leaf form and structure, but it closely resembles the remaining species, *M. huberi.* From the latter it differs chiefly in its fruit, which is roundish with a small smooth calyx scar. The smooth scar apparently results from the fact that the hypanthium is circumscissile at its base, leaving little tissue on top of the enlarging ovary. In *M. huberi* the hypanthium is circumscissile ½–⅔ of the way from the base to the stamen attachment, leaving on the developing fruit a ring of tissue which becomes a broad circular inward-pointing rim 0.5–1 mm high. Apparently there is less expansion at the end of the developing fruit in *M. pranceana* than in *M. huberi,* and thus a smaller scar is produced in the former.

Other distinguishing features of the new species in comparison to *M. huberi* are the former's more acute blade apex and less grooved midrib above, its thicker leaves with higher stomatal crypts and more strictly columnar sclereids, its longer pedicels and larger calyx including the inferior ovary, its larger petals and anthers, its greater number of ovules, and its smaller seeds and hilum at least in the few examples checked.

It is a pleasure to name this plant for Dr. Prance, wide-ranging collector in Amazonia.

Mouriri cearensis Huber subsp. **carajasica** Morley, subsp. nov. TYPE: Brazil. Pará: Serra dos Carajás, Serra do Norte, ca. 20 km N of AMZA Exploration Camp (ca. 6°S, 50°15′W). In liana forest. Tree 15 m by 25 cm; corolla white. 18 Oct. 1977, *Berg, Henderson & Bahia BG 615* (holotype, MG; isotypes, MICH, NY, US).

Petioli alati 4.5–9 mm longi; laminae petiolis 11–17 plo longiores; lobi calycis 2.4–2.9 mm longi in sicco, ca. 2.6–3.2 mm longi in vivo; cicatrix calycis 4–6.5 mm diam. in fructu.

Tapering winged petiole 4.5–9 mm long, the lamina 11–17 times as long as the petiole; calyx lobes 2.4–2.9 mm long when dry, 2.6–3.2 mm long boiled and probably when fresh; calyx scar on dried fruit 4–6.5 mm diam.; seeds 9.5–11 mm high with a slight constriction about ⅓ of the way above the base, mostly dark brown above and below the constriction and medium brown at the constriction, the hilum 4–5 mm long, 2–3 mm wide.

Paratypes. BRAZIL. PARÁ: Serra dos Carajás: Marabá, caminho para o azul, bosquinho do aeroporto, (immature fr) 3 April 1977, *Silva & Bahia 3034* (NY, US); Serra Norte near AMZA Exploration Camp (ca. 6°S, 50°15′W), low forest on edge of steep slope, ca. 600 m, (fl) 11 Oct. 1977, *Berg & Henderson BG 469* (NY, US); vicintiy of AMZA headquarters, forest on terra firme, (fr) 17 Oct. 1977, *Silva et al. AS 43* (MICH, NY); Serra do Norte, ca. 20 km N of AMZA Exploration Camp, in liana forest, (fr) 19 Oct. 1977, *Berg & Henderson BG 638* (MICH, NY).

Distribution. Low forest or liana forest on terra firme in the Serra dos Carajás in southeast Pará, Brazil, at elevations of ca. 300 to 500 m.

Subspecies *cearensis* has the following contrasting characters: winged petiole 2–5.5 mm long, lamina (14–)18–30 times as long as the petiole, calyx lobes 3–3.8 mm long when dry, 3.2–4 mm long when boiled, calyx scar on dry fruit 7.5–10 mm diam., seeds 10.7–12.5 mm high, without a constriction, medium brown, the hilum 4–5 mm long, 3–3.4 mm wide.

Subspecies *cearensis* occurs near the coast in Ceará, Piaui, and Maranhão, disjunct nearly 600 km from the new subspecies, as the distributions are now known. Although subsp. *carajasica* is

distinct in morphology as well as being isolated geographically, in my estimation it is best regarded as a subspecies because there is little or no gap between the differing character-ranges of the two taxa and because of the great overall similarity in leaf anatomy, flower, and fruit in the two.

Mouriri viridicosta Morley, sp. nov. TYPE: French Guiana. St. Georges de l'Oyapock: Foret près de la Crique Gabaret. Arbuste de 6 m. Feuilles opposées à nervation peu visible. Fleurs fanées à calice jaune. Petits fruits jaunes. Nom local: Palikur: Bitkut kamwi. 22 Dec. 1978, *Lescure 834* (holotype, US; isotype, CAY; note on US label says *Lescure 834 = Oldeman B2731*). FIGURE 3.

Frutex 6 m altus; pagina inferior costae mediae foliae in sicco viridis; xylema costae mediae canaliculatum, non tubulare; sclerides foliorum filiformes; cryptae stomatophorae nullae; pedicelli 0.5–1.5 mm longi; calyx ovarium inferum includens 2.5 mm longus; ovarium 1-loculare, ovula 4; fructus 6.2–7.9 mm diam., stylo persistenti; semen 1, ca. 5 mm longum, 6.4 mm latum.

Shrub 6 m high; young twigs terete, gray. Petioles 1.5–2 mm long; blades 11–17.7 cm long, 3.3–5.6 cm wide, elliptic-oblong to ovate-oblong or elliptic-ovate-oblong, abruptly acuminate at the apex, acute at base; midrib grooved above, rounded below; lateral nerves faintly to moderately visible above when dry, faintly visible below; blade including the underside of the midrib a medium green when dry. Margins of the leaf midrib xylem extended and turned in and down but not fused to each other; stomatal crypts none; upper epidermis one cell thick; hypodermis none; mucilage walls none; free stone cells present only at base of midrib; terminal sclereids filiform, occasionally branching; tanniniferous compounds lacking. Flowers 1–several in crowded clusters at leafless nodes of twigs to 3 mm diam., the flowers 1 per peduncle, the peduncle ca. 0.5 mm long with a pair of short triangular bracts at top and bottom, the bracts 0.7–0.8 mm long. True pedicels 0.5–1.5 mm long; calyx including inferior ovary 2.5 mm long, campanulate, glabrous; calyx yellow; free hypanthium 1.2 mm long; calyx lobes low-triangular, 0.3–0.5 mm high, 1.2–1.4 mm wide, not separating further at anthesis. Mature petals unknown. Mature filaments unknown; anthers 1.2–1.4 mm long; sporangia 1.1–1.3 mm long, their mode of dehiscence unknown; gland 0.2–0.3 mm long, placed ca. 0.4 mm below the apex of the anther; cauda none. Ovary 1-locular with 4 ovules arranged around a short central and basal placenta; style 2.8–3 mm long. Fruits yellow, subglobose, 5.7–6.2 mm high, 5.9–6.7 mm diam. when dry, estimated 7–8.5 mm diam. when fresh, crowned with the remains of the hypanthium and calyx and with the persistent style. Seed 1, ca. 5 mm high, 6.4 mm wide, 2 mm thick, the polished center part (the enlarged outer face of the ovule) ca. 2.3 mm wide, the rest of that face of the seed wrinkled irregularly with subparallel lines radiating away and upward from the polished center.

Distribution. Known only from the type locality in tropical forest near the Oyapock River in east French Guiana at about 40 m elevation.

The seed of *M. viridicosta* unmistakably places this species in the subgenus *Taphroxylon,* where its non-tubular midrib xylem also fits best. However, within this subgenus the new plant has no close relatives. Even its section is uncertain. The evergreen habit, short pedicel, single tiny flower, and seed structure exclude it from section *Abundiflos.* The lack of tannins and the form and structure of the anther are agreeable with section *Taphroxylon,* but this relation is disputed by the limited distribution of the free stone cells and by the filiform sclereids, very short pedicel, tiny flower, and separate calyx lobes.

Of the present sections the new species is most at home in *Brevipedillus.* The limited distribution of the free stone cells, very short pedicel, tiny flower, and separate calyx lobes are all matched in this section, and even the filiform sclereids are approached in *M. duckeana* and *M. duckeanoides.* However, the lack of tannins and the anther form and structure are discordant.

To some extent the new species breaks down the boundary between *Taphroxylon* and *Brevipedillus.* A case could be made for placing it in a section of its own, since the fully filiform sclereids, small number of ovules, persistent style, and small fruit and seed are unique in the subgenus. However, because the majority of the known distinguishing characters for sections fall into an existing section, I am inclined to view *M. viridicosta* as an aberrant member of section *Brevipedillus* until further evidence indicates otherwise.

The persistence of the style on the fruit was known previously only in *Votomita monantha*; I had thought this might be a generic character for *Votomita,* but was mistaken.

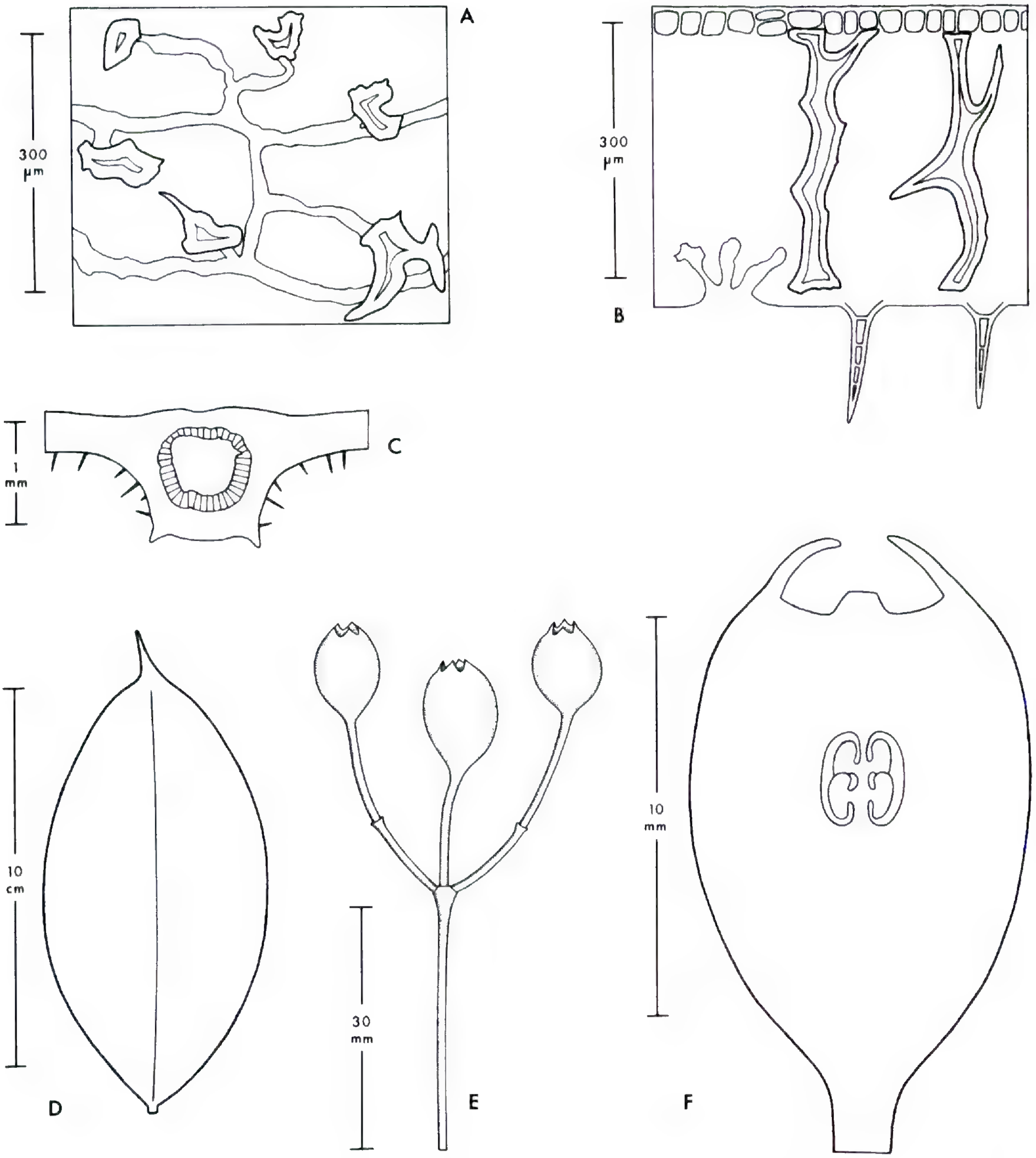

FIGURE 4. *Votomita pubescens* (*Lao M. 22*).—A. Cleared portion of leaf blade showing terminal sclereids and veins.—B. Cross section of leaf blade showing upper epidermis, sclereids, stomatal crypts, and hairs.—C. Cross section of leaf midrib.—D. Leaf.—E. Inflorescence.—F. Long section of flower.

Votomita pubescens Morley, sp. nov. TYPE: Peru. Loreto: Requena, Sapuena, Jenaro Herrera, 120 m. Collection from the Dep't. of Forest Management, Natl. Agric. Univ. at La Molina, Lima. Tree number R-D12 JH. "Lanza caspi." Arbol; bosque humedo tropical. 1970, *Rafael Lao M. 22* (holotype, F). FIGURE 4.

Arbor; folia supra glabra, subtus pubescentia; scleride foliorum terminales et columnares; sepala 4; ovarium 10.3–13.3 mm longum, tantum parvum contractum in sicco, in sicco laeve, induratum, olivaceum, duplo crassius ad placentas quam ad apicem, 2-loculare, placentis 2 in quoque loculo.

Tree. Petiole 5–6.5 mm long; blades 12–14 cm long, 5.8–6.5 cm wide, elliptic or slightly elliptic-ovate, abruptly caudate at the apex with a cauda 11–13 mm long, medium acute at base, glabrous above, pubescent beneath; midrib nearly plane above but with a slight groove down the center,

prominent below, the latter part rounded at base but soon 2-angled with 2 very narrow wings for its length, pubescent on the sides; lateral nerves not visible above or below when dry. Stomatal crypts multiple, each branched above the mouth into 2–7 small cavities, the multiples 90–175 μm total diam., 65–87 μm deep, averaging 35 per mm^2; upper epidermis mostly 1 cell thick, occasionally 2, of large square cells as seen in section; mucilaginous walls none; hypodermis none; foliar sclereids terminal, irregularly columnar, usually with an irregular short-branched central body and a dendroid branching system against each epidermis; hairs 80–190 μm long, apparently 1-celled but with 1–6 septae and an expanded base set in the epidermis. Peduncles axillary, 1 per side, each 2–3-flowered, 19–27 mm long to base of farthest pedicel measured along the axes and with 1 or 2 internodes in that length; bracts unknown, deciduous before anthesis. True pedicels 8–10 mm long; flowers 4-merous; calyx including inferior ovary 10.3–13.3 mm long, 7.8–9 mm thick, glabrous, shrinking only slightly on drying, when dry with a hard smooth somewhat polished olive green outer layer, the ovary about twice as thick at the midpoint as at the apex; calyx lobes separate, 0.9–2 mm long, 2.4–2.7 mm wide, triangular and slightly apiculate, not separating further at anthesis. Petals and stamens unknown. Ovary 2-locular, each locule with 2 axile placentas and an irregular very incomplete ridge running down the outer wall representing a missing partition; ovules 5–6 per placenta; style unknown, apparently deciduous at anthesis. Fruit and seed unknown.

Distribution. Known only from the type locality in a humid tropical forest in northeast Peru in the drainage of the Ucayali River at an elevation of 120 m.

The previously known species of *Votomita* form two groups, three species (*V. plerocarpa, V. monadelpha, V. orbinaxia*) with (3–)4 locules and 36–48 ovules and three species (*V. guianensis, V. orinocensis,* and *V. monantha*) with one locule and 5–10 ovules.

The new species falls in between these groups, because it has two locules (with two placentas in each) and 20–24 ovules. It is not similar to any of the other six. However, it is doubtless closest to the first group because of the four placentas and the fact that two of the first group (*V. plerocarpa* and *V. monadelpha*) have pubescent midribs, although not laminas. From the latter two species *V. pubescens* differs in its columnar terminal sclereids as well as in the characters that set it apart from all the other six species: the pubescent lamina, the ovary that is twice as thick at the midpoint as at the apex and that is smooth and hard when dry, and the two locules with a total of 20–24 ovules.

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NEW SPECIES OF *SOLANUM* SECTION *GEMINATA* (G. DON) WALP. (SOLANACEAE) FROM SOUTH AND CENTRAL AMERICA[1]

SANDRA KNAPP[2]

ABSTRACT

Four new species of *Solanum* section *Geminata* are described: **S. pastillum, S. heleonastes, S. dasyneuron,** and **S. aphyodendron.** Two of these are Central American, one from Guatemala and one from Costa Rica. The third is only found along the Río Paraná along the border of Argentina and Paraguay. The fourth is a widespread species that has long been confused with *S. nudum* H.B.K. ex Dunal. Nomenclature and details of natural history are discussed.

Solanum section *Geminata* (G. Don) Walp. is one of the largest sections in the genus, with approximately 70 species, all but one of which is exclusively neotropical. The section has previously been known as section *Leiodendra* Dunal (D'Arcy, 1972), but for reasons of priority (Knapp, 1983), *Geminata* (G. Don) Walp. is the correct sectional name for this species group.

Members of section *Geminata* are generally small trees or shrubs, often growing in the primary forest understory, an unusual habitat in the genus *Solanum.* Species in the section share difoliate nodes with many (but not all, see Danert, 1967; Child, 1979) other Solanums, which in section *Geminata,* as the name implies, are often geminate. In this situation the two leaves of the node arise from the same height on the stem due to failure of mesopodial elongation (Danert, 1958): therefore the subtending leaf of the previous shoot generation is at the same level as its daughter shoot. The leaves in a geminate cluster can be of equal size and shape or can differ in one or both of those characters. The most common situation in section *Geminata* is for the geminate cluster to be anisophyllous. The larger of the two leaves is termed the *major* leaf and the smaller the *minor* leaf. Section *Geminata* is further characterized by the leaf-opposed nature of the inflorescence, which also arises from the same level on the stem as the geminate leaves. This "leaf-opposedness" is due to meso- and epipodial suppression and adnation of the stem and the peduncle (Danert, 1967; Child, 1979) and is not perfect in all species. Pubescence in the section is absent or consists of uniseriate trichomes ("finger hairs" sensu Seithe, 1962, 1979), but branched trichomes do occur. The flowers are small, white or greenish white, and the degree to which the petals reflex at anthesis is often a good specific character. Fruits of most species are green and remain hard until the day of maturity, when they become soft and yellowish (pers. observ.), but several species have brightly colored, presumably bird-dispersed fruits. The pedicel scars of flowers that fall off without producing fruit become corky and are prominent in later stages of inflorescence growth. The spacing and arrangement of these scars is generally an overlooked character (but see D'Arcy, 1973) and is useful in distinguishing the species of section *Geminata.*

While preparing a revision of *Solanum* section *Geminata,* I have discovered several new species, both in the herbarium and in the field. Four of these are described here. Further details of the natural history of *S. pastillum* and *S. aphyodendron* can be found in Knapp (1985).

Solanum pastillum S. Knapp, sp. nov. TYPE: Costa Rica. Puntarenas: Monteverde, Camp-

[1] I thank W. G. D'Arcy, R. L. Dressler, W. Haber, B. Hammel, W. J. Kress, J. Mallet, M. Nee, and M. D. Whalen for helpful discussions and field assistance; Carol Kalafatic for preparing the illustrations; Missy Holbrook and Jack Putz for field assistance, and W. J. Dress for help with the Latin diagnoses. I thank the curators of the following herbaria for access to their specimens: BH, CR, F, G, LL, MO, NY, P, RSA/POM, TEX, US, USM, WIS. Field work in Costa Rica was funded by an Organization for Tropical Studies Inc. Jessie Smith Noyes Fellowship and a Sigma Xi Grant-in-Aid for Research; permission to collect and work in the Monteverde Cloud Forest Reserve was kindly granted by the Tropical Science Center, San José. Field work in Panama was funded by NSF grant DEB 79-22192 to W. G. D'Arcy of the Missouri Botanical Garden. The support of these institutions is gratefully acknowledged.

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FIGURE 1. *Solanum pastillum* (from *Knapp, Holbrook & Putz 6063*).

bell's Woods, 1,450 m, 20 Aug. 1982, *Knapp, Holbrook & Putz 6063* (holotype, BH; isotypes, CR, F, MO, US). Figure 1.

Frutex gracilis; *caules* virides petiolorum basibus leviter alati; *folia* ovata geminata utrinque glabra subtus pallide viridia, apice acuminato, basi attenuata decurrente; *inflorescentiae* foliis opposita simplices glabrae pendulae; *pedicelli* sub anthesi deflexi; *calycis lobi* orbiculati succulenti 1 mm diam.; *corolla* rotata dilute viridi-alba, lobis reflexis carinatis; *bacca* globosa flavoviridis, pedicello lignoso infra calycis tubum expanso; *semina* ovoidea reniformia fulva, testa foveolata.

Slender arching shrubs, 1–3 m tall; stems glabrous, green, horizontally spreading, winged between the nodes with the decurrent leaf bases; bark of the older stems pale green, white-lenticellate. Leaves geminate, elliptic-ovate, widest at or just below the middle, dark green and slightly bullate above, pale sea green beneath, glabrous; major leaves 11.2–22 cm long (occasionally to 25 cm on the lower branches), 3.4–6.6 cm wide (to 11.3 cm on the lower branches), with 6–8 pairs of primary veins, raised above, paler and prominent beneath, the apex long acuminate, the base decurrent on the petiole, attenuate to cuneate; petioles 0.5–1 cm long; minor leaves differing from the major ones only in size, 2.1–6 cm long, 1.1–3.5 cm wide, the apex long acuminate, the base attenuate; petioles 3–5 mm long. Inflorescences opposite the leaves, simple, glabrous, translucent green, minutely white-lenticellate, 1.7–7 cm long, slender and pendulous, 5–50-flowered; pedicel scars irregularly spaced, 1–3 mm apart, beginning ca. 1 cm from the base of the inflorescence; pedicels at anthesis deflexed, 1.4–1.5 cm long, tapering from the calyx tube to a slender base ca. 0.5 m diam.; buds conical, the corolla soon exserted from the globose calyx lobes, glabrous; calyx tube ca. 1.5 mm long, broadly cup-shaped, translucent green, lobes on fresh specimens consisting of 5 orbiculate projections ca. 0.5 mm diam. on the rim of the calyx tube, in dry specimens of irregularly shaped projections 0.5–1 mm long from the rim of the calyx tube, glabrous and translucent green; corolla greenish white, 1.1–1.2 cm across, lobed ca. three-fourths of the way to the base, the lobes reflexed at anthesis, the tips of the lobes carinate-hooded, minutely papillose; anthers 2.5–3.25 mm long, 1.25–1.5 mm wide, poricidal at the tips, the pores becoming slit-like upon drying; free portion of the filaments ca. 0.5 mm long, the filament tube

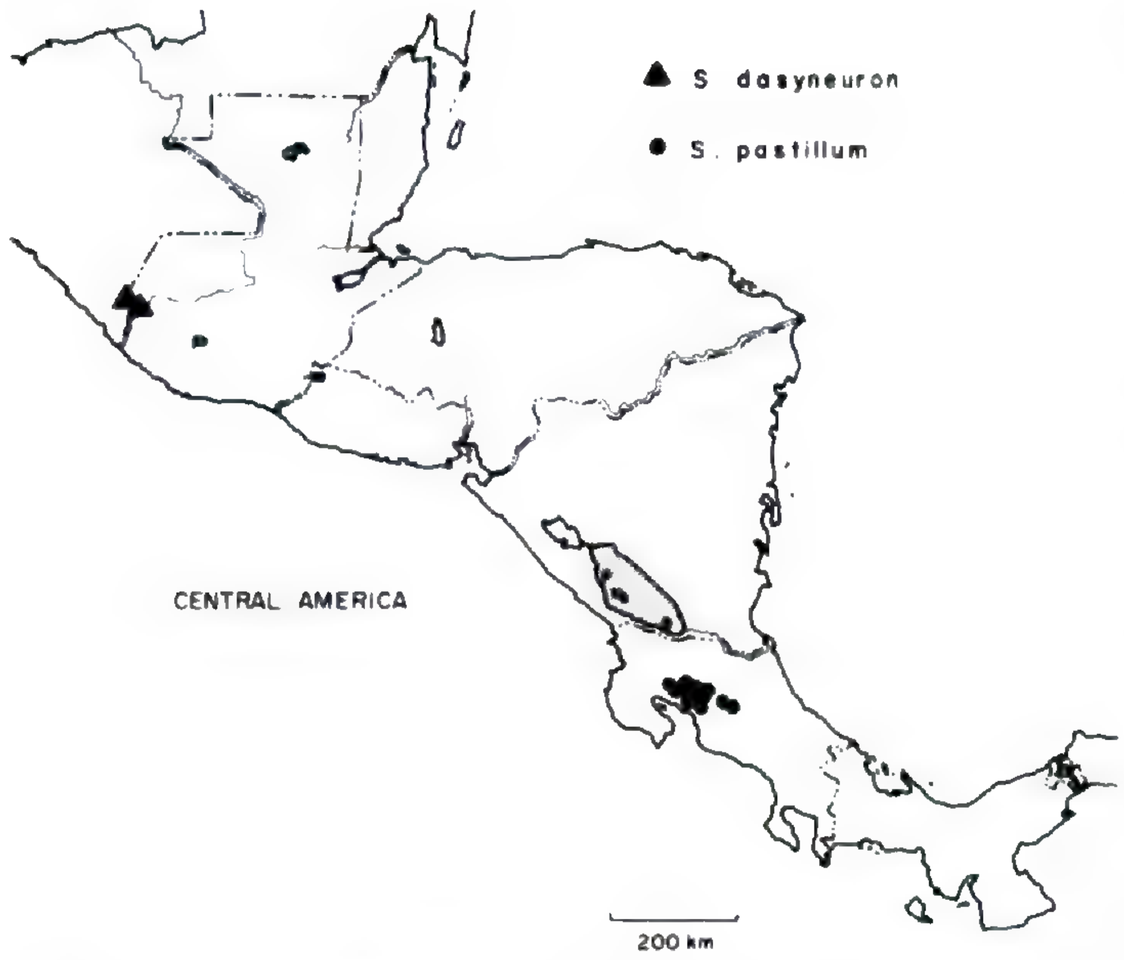

FIGURE 2. Distribution of *Solanum pastillum* and *Solanum dasyneuron*.

ca. 0.5 mm long; ovary glabrous; style 5–6 mm long, straight or curved in dry specimens; stigma capitate, minutely papillose. Berry globose, greenish yellow at maturity, ca. 50-seeded, 1–1.5 cm diam., usually only 1 or 2 from an inflorescence; fruiting pedicels 1.9–2.6 cm long, woody, deflexed, greatly expanded at the distal end, there ca. 4–7 mm diam., the base slender, ca. 0.5 mm diam.; seeds pale brown or tan, ovoid reniform, 3.5–4 mm long, 2–2.5 mm wide, the surfaces minutely pitted, the pits very shallow, the seeds appearing smooth. Chromosome number, $n = 12$ (Knapp, unpubl. data; voucher, *Knapp et al. 6063*).

Distribution. Found only in the cloud forests of montane central Costa Rica from 1,000 to 1,700 m. Figure 2.

Solanum pastillum is an isolated species in section *Geminata*. The most probable close relative of *S. pastillum* is *S. tuerckheimii* Greenm., also of montane central Costa Rica (but extending into Nicaragua, Guatemala, and Mexico). The two species share the understory habitat, long inflorescences of greenish white flowers with reflexed petals at anthesis, and hard green fruits which become yellow and soft upon maturity.

Solanum pastillum blooms at the beginning of the wet season at Monteverde de Puntarenas, Costa Rica, the type locality, and is pollinated primarily by bumblebees, *Bombus ephippiatus* (Knapp, 1985). The local distribution pattern of *S. pastillum* is typical of many of the forest understory species of section *Geminata*. Small clumps of three to five individuals grow at widely spaced intervals in the understory, often at the edges of old gaps caused by fallen trees or branches. The inflorescences of *S. pastillum* are many-flowered, but only a few fruits per inflorescence develop. Whether this is due to poor pollination success or to fruit abortion is not known. The presence of a single fruit on a long inflorescence causes the effective pedicel length of the fruit to be extremely long. This may make the fruit more visible to small frugivorous bats, known to take the fruits of this and many other species of section *Geminata* in Monteverde (E. Dinerstein, pers. comm.).

The specific epithet, "pastillum" meaning small round loaf of bread, refers to the orbiculate calyx lobes, which are quite distinctive in this species.

Additional specimens examined. COSTA RICA. ALAJUELA: Llanura de San Carlos, 100 m, 21 Feb. 1966, *Molina R. et al. 17659* (F); Peñas Blancas Trail, 3.5–5 km ESE of Monteverde, ca. 1,450 m, 17 Aug. 1976, *Kennedy & Guindon 3713* (F); Monteverde, on road to Peñas Blancas (over Continental Divide) ca. ½ km below the Divide on Atlantic slope, 1,450 m, 10°25′N, 84°50′W, 13 Apr. 1981, *Knapp & Mallet 864* (BH); Alfaro Ruíz, Guadelupe de Zarcero, 1,550 m, 1 July 1938, *Smith NY810* (F, NY); Alfaro Ruíz, La Peña de Zarcero, 1,400 m, 11 July 1938, *Smith NY904* (F, NY); Alfaro Ruíz, Zapate, 1,425 m, 10 May 1940, *Smith P2663* (F); Alfaro Ruíz, 5 mi. S of Zarcero, 1,500 m, 17 June 1941, *Smith 2789* (F). CARTAGO: El Muñeco on Río Navarro, 1,400–1,500 m, 6–7 Mar. 1926, *Standley & Torres R. 51016, 51040* (US). PUNTARENAS: Sendero El Brillante, Monteverde Cloud Forest Reserve, 1,450–1,500 m, 13 May 1976, *Dryer 81* (F); S of the road, Monteverde Cloud Forest Reserve, 1,520–1,580 m, 16 June 1976, *Dryer 208* (F); Monteverde, near the Ventana (Continental Divide), 1,500–1,600 m, 12 July 1976, *Dryer 426* (F); S of road, Monteverde Cloud Forest Reserve, 1,520–1,580 m, 28 Aug. 1976, *Dryer 683, 684* (F); Monteverde Cloud Forest Reserve, ½ km from the station along the Sendero Río, 1,500 m, 10°25′N, 84°50′W, 19 Feb. 1981, *Knapp 830* (BH); Monteverde Cloud Forest Reserve on Sendero Pantanoso near the Continental Divide, 1,600 m, 10°25′N, 84°50′W, 11 Mar. 1981, *Knapp 840* (BH). SAN JOSÉ: Santiágo de San Ramon, 1,150 m, 29 July 1937, *Brenes 22615* (F); 5 mi. S of Santa María, 6,800 ft., 5 Feb. 1928, *Stork 1757* (F).

Solanum heleonastes S. Knapp, sp. nov. TYPE: Argentina. Corrientes: Capital, Puerto Italia en montes costeros del Río Paraná, 6 Nov. 1972, *Schinini 5671* (holotype, MO; isotypes, MO, WIS). Figure 3.

Frutex vel arbor parva; *caules* juniores incani trichomatibus minutis uniseriatis dense pubescentes; *caules* veteres succulenti nitidi rubiginosi; *folia* ovata geminata supra glabra subtus in nervis minute papillata, nervis stramineus, apice acuto vel acuminato, basi

FIGURE 3. *Solanum heleonastes* (from *Schinini 5671*, fruit from *Schwindt 30*).

cuneata valde obliqua; *inflorescentiae* foliis opposita simplices modo caulium juniorum pubescentes; *pedicelli* sub anthesi erecti; *calycis lobi* longe acuminatae; *corolla* rotata alba, lobis planis leviter carinatis; *bacca* globosa lignosa, in specimenibus exsiccatus ochracea, pedicello lignoso erecto; *semina* fusca complanata reniformia, testa foveolata; *habitat* in paludibus fluvii Parana inter Argentina et Paraguay.

Shrubs or small trees, 1–5 m tall; young stems and leaves densely covered with appressed uniseriate papillate trichomes, 0.05–0.1 mm long, these irregular and floccose in appearance, greyish brown, the young growth with a grainy texture; bark of the older stems red-brown, shining, glabrate, minutely white-lenticellate. Leaves ovate, geminate, widest just below the middle, glabrous above, minutely papillate on the veins beneath, the veins yellowish, epidermis large-celled and appearing crystalline; major leaves 10.2–18.5 cm long, 5.8–7.9 cm wide, with 8–10 strong, evenly spaced primary veins, these yellow beneath, the secondary venation obscure, the apex acute or acuminate, the base broadly cuneate, strongly oblique; petioles 1.7–3.2 cm long, slightly winged from the decurrent leaf bases; minor leaves differing from the major ones only in size, 7–11 cm long, 3.4–5.5 cm wide, the apex acute or acuminate, the base broadly cuneate, attenuate, oblique; petioles 0.8–1.2 cm long. Inflorescences opposite the leaves, simple, 1–2 cm long, 10–30-flowered, densely covered with papillate trichomes as those of the young stems and leaves; pedicel scars closely and evenly spaced, but not overlapping; pedicels at anthesis erect, 1.1–1.4 cm long, tapering from the base of the calyx tube to a slender base ca. 0.5 mm diam., minutely white-speckled, sparsely papillate with uniseriate

FIGURE 4. *Solanum dasyneuron* (from *Matuda 2849*).

trichomes like those of the young stems and leaves; buds at first globose, enclosed in the urceolate calyx tube, later ovoid and exserted from the clayx tube; calyx tube 1.5–2 mm long, urceolate in bud, later cup-shaped, the lobes long triangular, 2.5–5 mm long, white-speckled, minutely papillose at the tips; corolla white (blue in *Schwarz 8182*), 1.2–1.5 cm across, lobed nearly to the base, the lobes planar at anthesis, tips of the lobes slightly carinate, minutely papillose at the tips and the margins; anthers 3.5–4 mm long, tightly connate in young flowers, 1–1.5 mm wide, poricidal at the tips, the pores becoming slit-like upon drying; free portion of the filaments ca. 1 mm long, the filament tube ca. 0.5 mm long; ovary glabrous; style filiform, 5–7 mm long, straight; stigma minutely capitate, white-papillose. Berry globose, dry and woody with very little pulp, 1–1.2 cm diam., mustard yellow in dried specimens, the septum between the carpels dry and papery in dry specimens; fruiting pedicels erect and woody, 1.1–1.4 cm long, ca. 1 mm

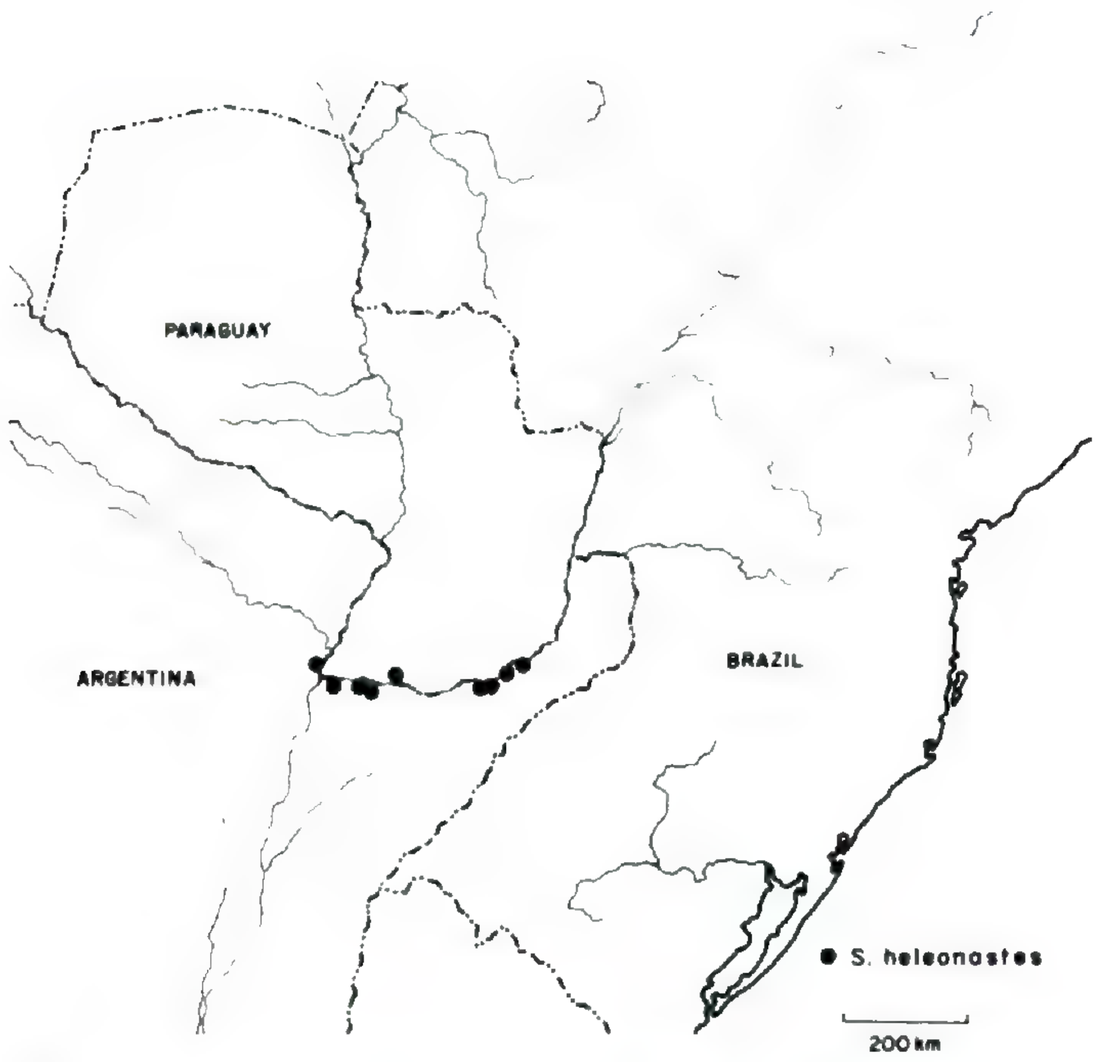

FIGURE 5. Distribution of *Solanum heleonastes*.

diam. at the base; calyx lobes becoming woody and reflexed in fruit; seeds dark brown, flattened reniform, ca. 2 mm long, 1.5 mm wide, the surfaces minutely pitted. Chromosome number, not known.

Distribution. Found only in the swampy forests on the margins and islands in the upper Rio Paraná, on the border between Argentina and Paraguay, from 100 to 200 m. Figure 5.

Solanum heleonastes is closely related to *S. robustifrons* Bitter of eastern Peru and adjacent Brazil, differing from that species in its longer calyx lobes, smaller leaves, and generally more pubescent young stems and leaves. *Solanum heleonastes* is usually a large tree, and *S. robustifrons* is a small shrub or treelet that grows in the understory of dense forests at middle elevations. *Solanum heleonastes* is one of the few species of section *Geminata* growing in swamp forest and is quite common in areas where it is found.

The specific epithet of this species, "heleo" meaning swamp and "nastes" meaning inhabitant, refers to the unusual habitat of this species.

Additional specimens examined. ARGENTINA. CHACO: 1° de Mayo, Col. Benítez, Bermejo, Isla Brasiliera, 4 Oct. 1964, *Schulz 9422* (F, WIS). CORRIENTES: Capital, on the Río Paraná 5 km from Corrientes, 10 Oct. 1944, *Hunziker 5700* (US); Arroyo Itaimbí, 15 Dec. 1944, *Sesmero 201* (NY); Capital, Puerto Italia, 27 July 1974, *Schinini & Gonzalez 9502* (MO, WIS); Ituzaingó, Isla San Martín, 9 Oct. 1949, *Schwarz 8182* (BH). MISIONES: Posadas, Río Alto Paraná, 18 Nov. 1907, *Ekman 820* (MO); Posadas, 17 Apr. 1930, *Rodríguez 188* (F); Candelaria, San Juan, 216 m, 4 Jan. 1947, *Schwindt 30* (RSA/POM). PARAGUAY: sin. loc., 1853–1856, *Palmer s.n.* (US).

Solanum dasyneuron S. Knapp, sp. nov. TYPE: Mexico. Chiapas: Volcán Tacaná, Chiquihuite, 2,800 m, 27 Mar. 1939, *Matuda 2849* (holotype, F; isotypes, F, NY). Figure 4.

Frutex; *caules* glabri in sicco nigrescentes aetate provecta albicantes; *folia* obovata vel anguste obovata geminata super glabra subter venis dense pubescentia, apice acuto, basi attenuata; *inflorescentiae* foliis opposita simplices vel interdum furcatae glabrae nitidae in sicco nigrescentes; *pedicelli* sub anthesi deflexi; *calycis lobi* succulenti deltoidei intus papillosi; *corolla* rotata alba succulenta, lobis planis, stigmate capitatum; *bacca* immatura globosa, pedicello lignoso deflexo; *habitat* in sylvis nubosis Volcan Tacana insidentibus inter Mexico et Guatemala.

Shrubs 2–3 m tall; young stems and leaves glabrous or occasionally minutely rusty-papillate, drying black and shiny; bark of older stems white, exfoliating in small transverse pieces. Leaves obovate to narrowly obovate, geminate, glabrous above, the midrib depressed, the primary veins raised, densely pubescent on the primary and secondary veins beneath with uniseriate trichomes 0.25–0.5 mm long, trichomes restricted to on the veins, none on the lamina; major leaves 12.5–17.3 cm long, 5–6.5 cm wide, with 11–15 pairs of primary veins, the apex acute, the base attenuate, not decurrent on the petiole; petioles 1.5–1.9 cm long; minor leaves differing from the majors only in size, 2.2–7 cm long, 1.6–2.9 cm wide, apex acute, the base attenuate; petioles 0.6–1.1 cm long. Inflorescences opposite the leaves, simple or occasionally once furcate, 1–5 cm long, 10–20-flowered, glabrous and shining; pedicel scars closely spaced and overlapping, beginning 4–6 mm from the base of the inflorescence; pedicels at anthesis deflexed or somewhat erect, 1.1–1.5 cm long, robust and somewhat fleshy, 0.75–1 mm diam. at the base, tapering imperceptibly to the calyx lobes; buds ovoid, fleshy, pointed and constricted apically, only partially exserted from the calyx; calyx tube 1.5–2.5 mm long, conical, the lobes deltoid, apiculate, 1–2 mm long, papillose within, glabrous without, the margins of the lobes white and thickened; corolla white, thick and fleshy, ca. 1.5 cm across, lobed nearly to the base, planar at anthesis, the lobes minutely papillose on the margins and tips, tips cucullate; anthers 3.5–4 mm long, 1–1.5 mm

FIGURE 6. *Solanum aphyodendron* (from *Knapp, Kress & Hammel 4136*).

wide, poricidal at the tips, the pores becoming slit-like upon drying; free portion of the filaments ca. 0.25 mm long, the filament tube ca. 0.5 mm long, drying black; ovary glabrous; style ca. 7 mm long, straight; stigma large and capitate, ca. 1 mm diam., minutely papillose. Berry globose, 8 mm diam. (immature), green; fruiting pedicels deflexed, woody, 1–1.5 mm diam. at the base; calyx lobes enlarging and becoming woody in fruit, ca. 4 mm long; seeds unknown. Chromosome number, not known.

Distribution. Endemic to the upper slopes of Volcan Tacana, on the border of Mexico and Guatemala, in wet forest from 2,500 to 3,000 m. Figure 2.

Solanum dasyneuron is closely related to *S. narcoticosmum* Bitter and *S. vacciniiflorum* Standley & Williams, both of montane Central America. *Solanum dasyneuron* differs from both of those species in its large fleshy flowers, thick pedicels, its tendency to dry blackish, and by the dense pubescence on the veins on the undersides of the leaves.

The species epithet, "dasy" meaning hairy and "neuron" meaning nerve, refers to the distinctive pubescence on the veins of the leaf undersides.

Additional specimen examined. GUATEMALA. SAN MARCOS: between La Vega ridge along Río Vega and NE slopes of Volcán Tacaná, to 3 mi. from Guatemala–Mexico border, in vicinity of San Rafael, 2,500–3,000 m, 20 Feb. 1940, *Steyermark 36198* (F, 2 sheets).

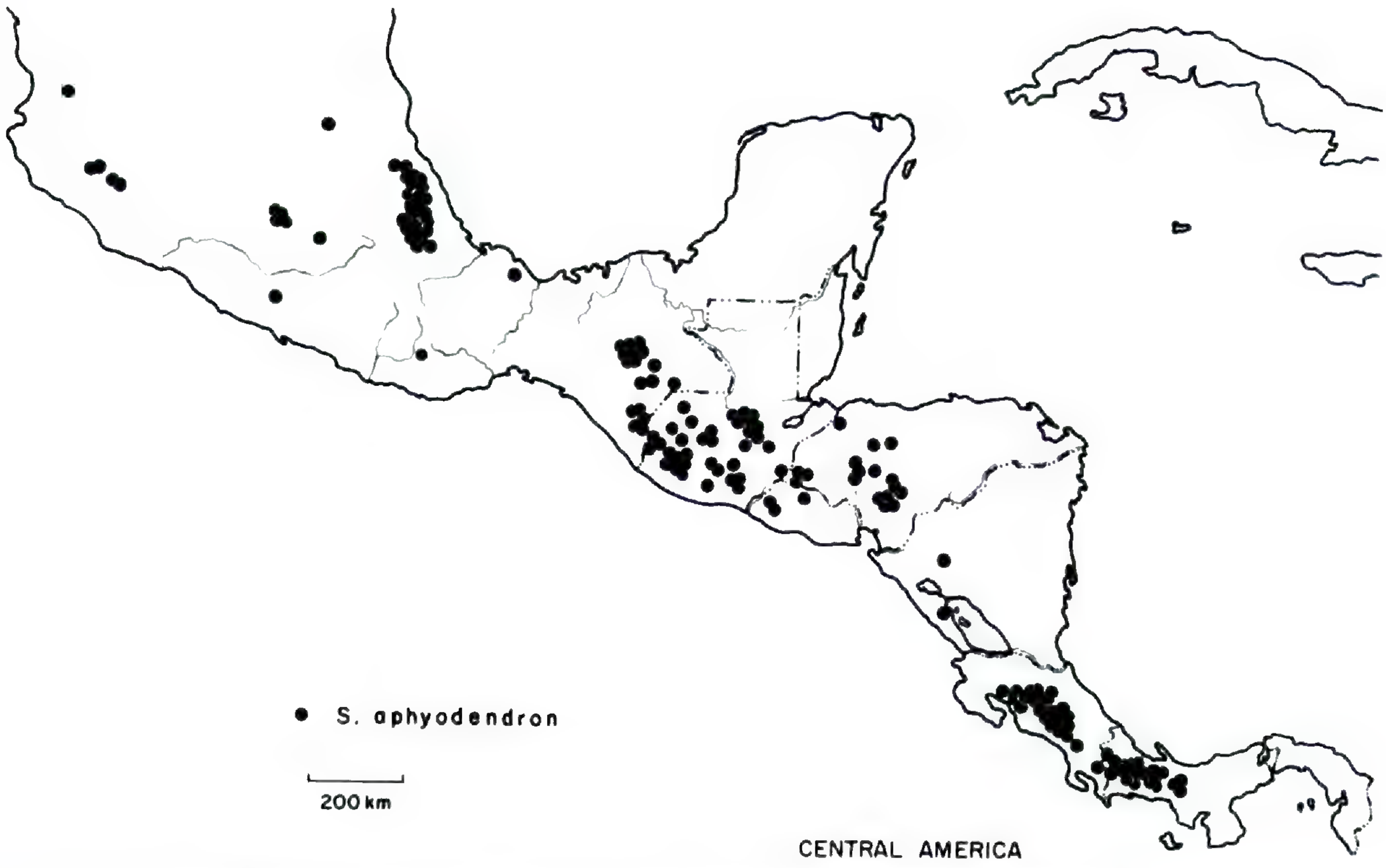

FIGURE 7. Distribution of *Solanum aphyodendron* in Central America and Mexico.

Solanum aphyodendron S. Knapp, sp. nov. TYPE: Panama. Chiriquí: along Quebrada Alemán, 8 mi. N of Los Planes de Hornito, IRHE Fortuna Hydroelectric Project, 1,200 m, 8°45'N, 82°12'W, 13 Mar. 1982, *Knapp, Kress & Hammell 4136* (holotype, BH; isotypes, MO, others to be distributed). Figure 6.

Bassovia foliosa Brandegee, Univ. Calif. Publ. Bot. 6: 373. 1917 non *Solanum foliosum* Link in Buch. TYPE: Mexico. Veracruz: Zacuapan, Dec. 1915, *Purpus 7565* (CAL, isotype, MO!).

Solanum nudum auct. non H.B.K. ex Dunal, Solan. Syn. 20. 1816.

Solanum parcebarbatum Morton & Standley, Publ. Field Mus. Nat. Hist. Bot. Ser. 18: 1088. 1938 pro parte, non Bitter.

Frutex vel arbor parva locos apertos habitantes; *caules* teretes virides glabri albescentes in sicco nigrescentes; *folia* anguste ovata geminata in sicco pallide viridia supra glabra subtus caespitibus trichomatum uniseriatarum in axillis nervorum pubescentia, viridi-albis, apice acuto vel acuminato, basi cuneata vel leviter attenuata et decurrento; *inflorescentiae* foliis oppositae simplices glabrae; *gemmae* globosae; *pedicelli* sub anthesi deflexi; *calycis lobi* deltoidei trichomatibus uniseriatibus pubescentes 1 mm longi; *corolla* rotata alba lobis sub anthesi reflexis; *bacca* globosa flavo-viridis, pedicello lignoso; *semina* fulva complanata reniformia, testa foveolata, marginibus incrassata.

Shrubs or small trees, 3–15 m tall; young stems and leaves glabrous or with a few scattered uniseriate trichomes, drying blackish; bark of older stems greenish white and rough; stems slightly winged from the decurrent petiole bases. Leaves narrowly ovate, geminate, widest at or just below the middle, drying pale greyish green, glabrous above and below, except for tufts of uniseriate trichomes in the axils of the primary veins beneath, the trichomes ca. 1 mm long, white; major leaves 8.5–15 cm long, 3–6.1 cm wide, with 8–10 pairs of primary veins, these depressed above, raised and pale greenish white beneath, the apex acute or acuminate, the base cuneate or slightly attenuate, with a small wing on the petiole; petioles 0.6–1.7 cm long; minor leaves differing from the major ones only in size, 3.2–8.6 cm long, 1–4 cm wide, the apex acute or acuminate, the base cuneate; petioles 4–8 mm long. Inflorescences opposite the leaves, simple, 1–2.6 cm long, 20–30-flowered, glabrous or occasionally with a few scattered uniseriate trichomes distally; pedicel scars closely spaced, occasionally overlapping, beginning ca. 1 cm from the base of the inflorescence; pedicels at anthesis deflexed, 0.7–1.1 cm long, tapering from the calyx tube to a slender base ca. 0.5 mm diam.; buds globose, the corolla soon exserted from the calyx, pubescent with uniseriate trichomes 0.1–1 mm long; calyx tube ca. 1 mm long, crateriform, the lobes broadly triangular, 0.5–1 mm long, densely to sparsely

pubescent with uniseriate trichomes 0.1–1 mm long, the margins of the lobes white and scarious; corolla white, often drying with a lavender tinge, 1–1.2 cm across, lobed nearly to the base, the lobes slightly reflexed at anthesis, tips and margins of the lobes minutely papillose; anthers 2.5–3 mm long, 1–1.5 mm wide, poricidal at the tips, the pores becoming slit-like upon drying; free portion of the filaments ca. 0.25 mm long, the filament tube ca. 0.5 mm long; ovary glabrous; style 5–7 mm long, straight; stigma not distinct from the body of the style, minutely papillose. Berry globose, bright green, ripening yellow-green, 1–1.2 cm diam., remaining hard until maturity, then softening overnight; fruiting pedicels deflexed, woody, 1.5–2.3 cm long, ca. 1 mm diam. at the base; seeds tan, flattened reniform, 2.5–3 mm long, 1.5–2 mm wide, the surfaces minutely pitted, margins incrassate, pitting of margins larger than that of the body. Chromosome number, $n = 12$ (Knapp, unpubl. data; voucher, *Knapp et al. 4136*).

Vernacular names. "Capulin de pajaro," "yerba de zopilote," Mexico; "zorrillo," Las Cruces, Puntarenas, Costa Rica; "kaqi sakyol," Quecchi language, Alta Verapaz, Guatemala; "huele de noche," Chiquimula, Guatemala; "hedionilla," Quezaltenango, Guatemala; "hiede hiede," Cerro Punta, Chiriqui, Panama.

Distribution. Widely distributed in second growth at middle to high elevations (800–2,500 m) from Mexico to Bolivia. Figures 7 and 8.

Solanum aphyodendron is a common species of roadsides throughout Central America and northern South America, and it often forms large monospecific stands in open areas. Material from Central America, Colombia, and Venezuela is quite uniform. Variability in pubescence increases in Peruvian and Bolivian specimens, with some specimens having shorter trichomes on the calyx lobes and denser trichomes in the vein axils.

In Monteverde de Puntarenas, Costa Rica, *Solanum aphyodendron* blooms at irregular intervals throughout the year (Knapp, 1985). Data from herbarium specimens and observations of this species in Panama indicate that its flowering behavior is very much the same throughout its range. At Monteverde, *S. aphyodendron* is pollinated by Meliponine bees, primarily by *Melipona fasciata* (Knapp, 1985). The occurrence of large monospecific stands of *S. aphyodendron* combined with the foraging behavior of *Melipona* produces high fruit set in this species. The ripe fruits are eaten by small frugivorous bats and disappear soon after they become ripe (E. Dinerstein, pers. comm.).

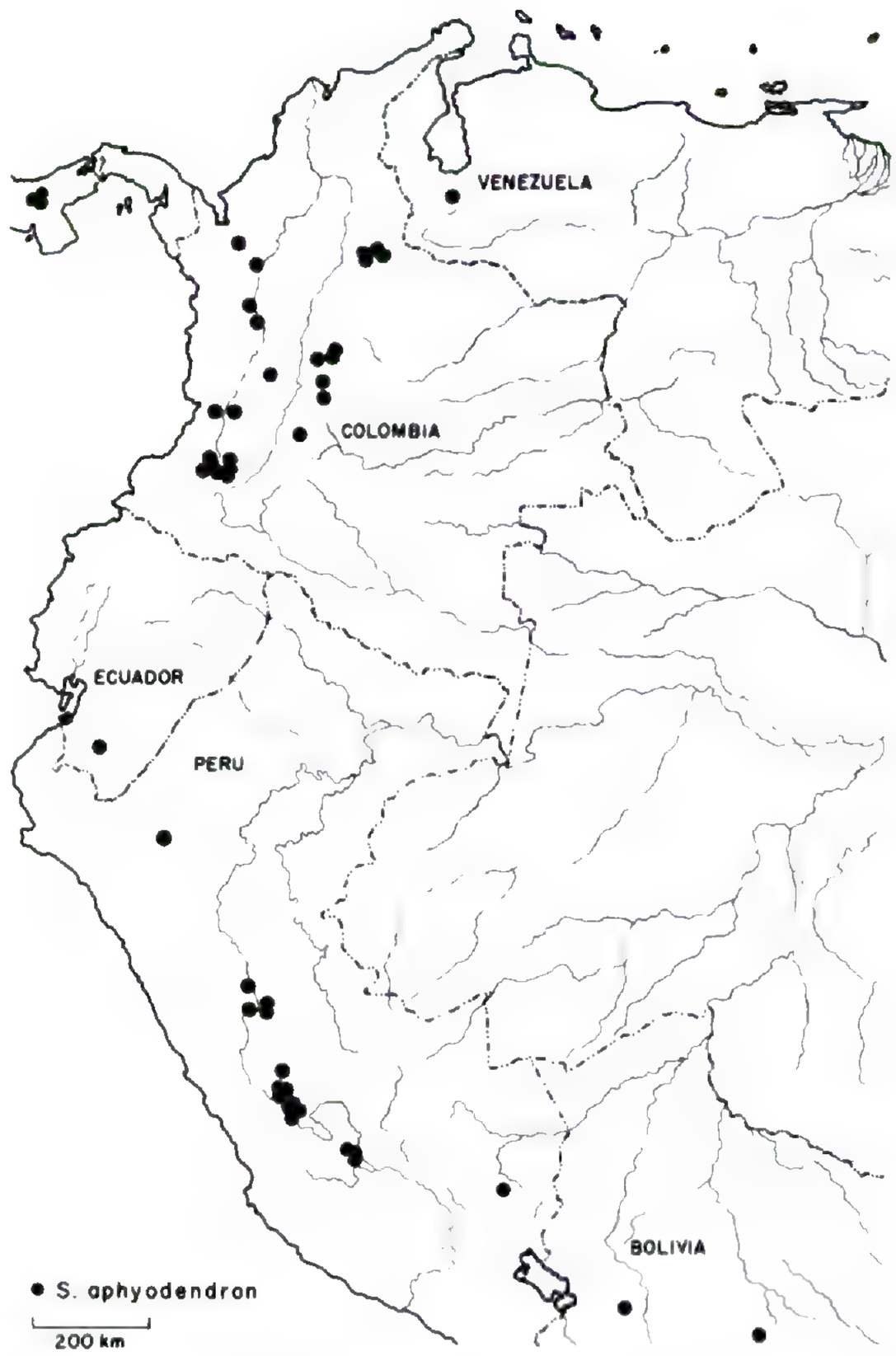

FIGURE 8. Distribution of *Solanum aphyodendron* in South America.

Solanum aphyodendron has long been confused with *S. nudum* H.B.K. ex Dunal, to which it is extremely closely related, but differs in habitat, flower size, pubescence of flower parts, and in the color and texture of the bark of older stems. *Solanum nudum* occurs in low elevation thickets, sometimes on beach strands, and has dark brown bark and glabrous, globose buds. The type specimen of *S. nudum* in the H.B.K. herbarium at Paris clearly belonged to the lowland, glabrous budded taxon, which left the pubescent, middle to high elevation taxon without a name. Brandegee's (1917) epithet "foliosa" unfortunately cannot be used, as an earlier homonym exists (*Solanum foliosum* Link in C. L. Buch, 1825). An unpublished name, *S. chamaecerasus* Bitter, has been applied to this species in a few herbaria,

but I have chosen not to use it, as inappropriate to the characteristics of the species.

This species is named for its distinctive whitish bark, "aphyo" meaning becoming white and "dendron" meaning tree.

Representative specimens examined. MEXICO. CHIAPAS: Tenejapa, paraje of Koltol Te', 4,750 ft., 10 July 1964, *Breedlove 6121* (US); Unión Juárez, Bosque de Pino, 1,360 m, 18 Nov. 1977, *Calzada et al. 3711* (F); along Mexican Hwy. 195, 2 mi. N of Colonia San José, 8 mi. S of Layón, 1,500 m, 3–4 June 1973, *Hansen et al. 1689* (BH, US, WIS); Mt. Tacaná, 1,000–2,000 m, Aug. 1938, *Matuda 2466* (F, US); Mt. Pastal, 12 Apr. 1948, *Matuda 17683* (F); near Finca El Suspiro, 11 Jan. 1953, *Miranda 7654* (US); near Tumbala, 4,000–5,500 ft., 20 Oct. 1895, *Nelson 3332* (US); Finca Mexiquito, July 1913, *Purpus 6980* (F, US); Cerro del Boquerón, June 1914, *Purpus 7318* [F (mixed collection with *S. narcoticosmum* Bitter), MO]; Tenejapa, paraje Balum K'aual, 8,400 ft., 13 Apr. 1966, *Shilom Ton 811* (F, LL, NY). GUERRERO: 5 km E of Omiltemi, Chilpancingo, 2,300 m, 1 Sept. 1962, *Rzedowski 16019* (US). HIDALGO: Chapulhuacan, 1,300 m, 12 July 1937, *Lundell & Lundell 7192* (LL, NY). JALISCO: SW foothills of the Nevado de Colima, ca. 10 mi. SW of Atenquique on the Tonila road, 1,600 m, 5 Apr. 1951, *McVaugh 11801* (NY, US); above Ahuacapán, road to Corralitos 10–12 mi. SSE of Autlán, 1,500–1,800 m, 29 Sept. 1960, *McVaugh 19586* (US); 12 mi. SW of Chante along road to Sierra Manantlan, 5,500 ft., 4 Feb. 1975, *Gentry & Gentry 23510* (US). MEXICO: Temascaltepec, Tejupilco, 1,340 m, 9 Apr. 1934, *Hinton et al. 5753* (LL, NY, US). MORELOS: Sierra de Ocuila, 18 Sept. 1941, *Lyonnet 3329* (US). NAYARIT: along Hwy. 28, between Tepic & Jalcatlán (Rt. 66 on some maps) at Km 14–16, 950–1,050 m, 8 Jan. 1979, *Croat 45256* (MO). OAXACA: 10 mi. S of Sola de Vega along road to Puerto Escondido, 7,000 ft., 8 May 1965, *Breedlove 9855* (US). VERACRUZ: Huatusco, road to Tepampa 4 km from the hwy. between Huatusco & Coscomatepec, 1,580 m, 14°10'N, 97°00'W, 10 Aug. 1979, *Avendaño & Calzada 411* (F); environs of Orizaba, *Bottieri & Sumichrast 1857* (P); Jalapa, 6 Sept. 1936, *MacDaniels 934* (BH, F); Xico, 6 km NE of Xico, 1,500 m, 19°27'N, 97°01'W, 12 May 1973, *Marquez & Gandara 101* (F); near La Calavera, 10 km N of Altotonga (13 km by road) on road to Tlapacoyan, 1,350 m, 19°51'N, 97°13'W, 28 June 1980, *Nee & Hansen 18643* (BH, F); 2.5 km (by road) E of Ayahualulco & 1.6 km (by road) W of Ixhuacán de los Reyes, 1,900 m, 19°2'N, 97°08'W, 7 Nov. 1981, *Nee 22959* (F); Jilotepec "El Esquilón," 1,390 m, 7 Jan. 1976, *Ortega et al. 104* (F, MO); Cerro de la Martinica, NE of Banderilla, 1,680 m, 10 Feb. 1976, *Ortega et al. 152* (F, MO); Los Reyes, 1,600 m, 22 Mar. 1976, *Vasquez S. 311* (F, NY); Tlazololapan, Tequila, 1,170 m, 29 Mar. 1976, *Vasquez T. 358* (F, NY); Yecuatla, Lomas de Santa Rita, 1,350 m, 3 June 1971, *Ventura A. 3268* (F); Atzalán, La Florida, 1,600 m, 20 Mar. 1978, *Ventura A. 15102* (F). GUATEMALA. ALTA VERAPAZ: near Cobán, 1,260–1,440 m, 26 Mar.–15 Apr. 1939, *Standley 69240* (F, US); 3 km W of San Julián, Tactic, 1,600 m, 15°20'N, 90°15'W, 1 Feb. 1969, *Williams et al. 40415* (F). BAJA VERAPAZ: below Patal, 1,550 m, 4 Apr. 1941, *Standley 90958* (F). CHIMALTENANGO: road to Iximche Ruins, Tecpán, 2,500 m, 12–23 Jan. 1966, *Molina R. et al. 16128* (F, NY). CHIQUIMULA: Cerro Brujo, vicinity of Río Negro, below Montaña Montenegro, near village of Brujo, 1,500–2,000 m, 1 Nov. 1939, *Steyermark 30939* (F, US). EL PROGRESO: Sierra de las Minas, between El Jute de Cobara & Finca Piamontes, 1,400–2,400 m, 3 Feb. 1942, *Steyermark 43381* (F, NY). ESCUINTLA: between Santa María de Jesús & Palin, 1,800 m, 29 Dec. 1938, *Standley 61307* (F, US). GUATEMALA: Km 28 F.D.R. between San Lucas & Guatemala City, 2,000 m, *Molina R. et al. 16657* (F, TEX). HUEHUETENANGO: 3 mi. NW of Santa Cruz Barillas along road to San Mateo Ixtatlán, 6,000 ft., 7 Aug. 1965, *Breedlove 11651* (F); Chiantla, 6,700 ft., 15 Dec. 1934, *Skutch 1949* (F, NY, US); 13 km W of Huehuetenango near Puente de Xinaxó, 1,800 m, 30 Dec. 1940, *Standley 81575* (F, US); spring of Río San Juan near Aguacatán, 1,800 m, 6 Dec. 1962, *Williams et al. 22501* (F, NY, US, WIS). QUEZALTENANGO: Los Positos SW of San Martín Chile Verde, 1,500 m, 8 Mar. 1939, *Standley 67901* (F, US); vicinity of Fuentes Georginas, slopes of Volcán de Zunil, 2,300–2,500 m, 3 Feb. 1941, *Standley 85865* (F, US); W slopes of Volcán de Zunil, opposite Santa María de Jesús, 1,500 m, 21 Jan. 1940, *Steyermark 35124* (F). SACATEPEQUEZ: near Pastores, 1,560–1,650 m, 14 Dec. 1938, *Standley 59937* (US). SAN MARCOS: Finca Vegel, near Rodéo, 900 m, 15 Mar. 1939, *Standley 68906* (F); barranco of Río (Tonana) Suchatí between Canjulá & La Unión Juárez, near SE portion of Volcán Tacaná, 2,000–3,000 m, 2 Feb. 1940, *Steyermark 36278* (F). SANTA ROSA: Jumaytepeque, 6,000 ft., Aug. 1892, *Heyde & Lux 4105* (F, MO, NY, US); near El Molino, 600 m, 26 Nov. 1940, *Standley 78379* (US); Volcán Tecuamburro, along trail to San Francisco Tecuamburro on summit of volcano, N of Chiquimulilla, 250–2,000 m, 20 Dec. 1939, *Steyermark 33149* (F). SUCHITEPEQUEZ: SW lower slopes of Volcán de Zunil between Finca des Asturias & Finca Alto Mira, NE of Pueblo Nuevo, 1,000–2,000 m, 1 Feb. 1940, *Steyermark 35349* (F). HONDURAS. COMAYAGUA: Montaña Le Choca, Cordillera Comayagua, near Coyocutena, 1,200 m, 22 May 1956, *Molina R. 7113* (F); Montaña El Cedral, Cordillera Montecillos, 1,600 m, 24 May 1956, *Molina R. 7194* (F, US); El Rincón, ca. 10 mi. W of Siguatepeque, 1,400–1,500 m, June–Aug. 1936, *Yuncker et al. 6050* (F, MO). CORTES: near Corinto, border with Guatemala 55 km W of Puerto Cortés, 9–11 Aug. 1975, *Nelson et al. 2936* (MO). MORAZÁN: Mt. San Juancito, 7,000 ft., 19 June 1948, *Glassman 1666* (F, NY, TEX, WIS); Cerro de Uyuca, 1,600–2,000 m, 10–20 Mar. 1951, *Morton 7167* (US). OCOTEPEQUE: around Belen Gualcho, 40 km E of Nueva Ocotepeque, 1,500–2,000 m, 29 June–3 July 1976, *Nelson et al. 3817* (MO). YORO: El Portillo Grande, 4,000 ft., July 1937, *van Hagen & van Hagen 1006* (F, NY); Quebrada Olotillo, 15 km from Yoro, 1,100 m, 8 May 1956, *Molina R. 6829* (US). EL SALVADOR. CHALATENANGO: E slope of Los Esemiles, 2,100–2,300 m, 14°21'N, 89°09'W, 1 Apr. 1942, *Tucker 1186* (F, LL). SANTA ANA: along road to Cerro Monte Cristo at Los Planes at Km 22, 1,800 m, 31 July 1977, *Croat 42332* (MO). SONSONATE: Cerro Verde, 1,800 m, 25 Feb. 1968, *Molina R. & Montalvo 21726* (F, NY). NICARAGUA. GRANADA: Mombacho Volcano, 960 m, 5 July 1923, *Maxon et al. 7781* (F, US). JINOTEGA: along

Hwy. 3 from Jinotega to Metagalpa, 5–8 mi. SW of Jinotega, 1,500 m, 7 Aug. 1976, *Croat 43055* (MO). COSTA RICA. ALAJUELA: Finca de los Ensayos ca. 11 mi. NW of Zarcero, 850 m, 15 Aug. 1977, *Croat 43541* (MO); along Río Alajuela, Alajuela–Carrizal road 5 km S of Carrizal, 1,200 m, 24 Mar. 1974, *Hartshorn 1423* (F, MO); Monteverde, road to Peñas Blancas (over Continental Divide) ca. 1 km below the Divide, Atlantic slope, 1,400 m, 10°25′N, 84°50′W, 13 Apr. 1981, *Knapp & Mallet 865* (BH, CR, to be distributed); Santa María National Park, Caribbean slope, 600 m, 10°27′N, 85°17′W, 7 Feb. 1978, *Leisner 5139* (MO); Zarcero, Palmiras, 6,000 ft., 16 Aug. 1937, *Smith A152* (F, MO, US); San Carlos, Sucre, 1,025 m, 2 Mar. 1939, *Smith H1638* (F, US); Naranjo, 5,600 ft., 5 Apr. 1928, *Stork 1852* (F). CARTAGO: Cartago, 1,650 m, Dec. 1887, *Cooper 5868* (F, US); overlooking Río Grande de Orosí, ca. 3 km SE of Tapantí, 1,350 m, 16 Apr. 1967, *Lent 832* (F, WIS); 5 km SW of Tobosí, 1,900 m, 9°50′N, 84°01′W, *Lent 3160* (F, MO); El Muñeco on the Río Navarro, 1,400–1,500 m, 6–7 Mar. 1926, *Standley & Torres R. 50939* (US); near La Sierra ca. 25 km S of Cartago, Cordillera de Talamanca, 2,000 m, 23 Jan. 1965, *Williams et al. 28048* (F). GUANACASTE: along road between Santa Elena & Monteverde, ca. 2 mi. from Santa Elena–Monteverde junction, 1,350 m, 7 Feb. 1979, *Croat 47100* (BH, MO). HEREDIA: vicinity of Alto la Palma between Paracito & Bajo La Hondura, 1,500 m, 14 Jan. 1978, *Croat 44484* (MO); Vara Blanca de Sarapiquí, N slope of Central Cordillera, 1,500–1,750 m, July–Sept. 1937, *Skutch 3286* (MO, NY, US). PUNTARENAS: Monteverde, pasture edges in village, 1,400–1,500 m, 15 Aug. 1976, *Dryer 566* (CR, F); Finca Las Cruces, 3 km S of San Vito de Java, 4,000 ft., 11 Feb. 1971, *Gillis & Plowman 10129* (F, TEX). SAN JOSE: Los Angeles de San Ramón, 1,075 m, 20 Nov. 1923, *Brenes 3947* (CR, F); La Palma, 1,250 m, 10 Sept. 1924, *Brenes 4063* (CR, F); near Quebrada Grande, 3 km NW of Cascajal, 1,750 m, 12 Dec. 1971, *Lent 2295* (F, MO); hills above Aserri, 14 June 1955, *Schubert & Rogerson 701* (US); vicinity of El General, 1,430 m, Dec. 1936, *Skutch 2987* (MO, NY, US); Río Segundo, 2,000 m, 10 May 1840, *Tonduz 1795* (US); Río Candelaria, 1,215 m, Apr. 1893, *Tonduz 7892* (US). PANAMÁ. CHIRIQUÍ: trail from Paso Ancho to Monte Lirio, upper valley of the Río Chiriquí Viejo, 1,500–3,000 m, 16 Jan. 1939, *Allen 1492* (F, MO, NY, US); Cerro Colorado, 1,500 m, 26 July 1976, *Antonio 1502* (MO); above Boquete, 4,500 ft., 12 May 1971, *D'Arcy 5443* (F, MO, P); roadside between Nueva California & Río Chiriquí Viejo, 7 Aug. 1972, *D'Arcy & D'Arcy 6492* (F, MO, NY, P, RSA/POM, WIS); Cerro Hornito, 4,500 ft., 8 May 1978, *Hammel 3028* (MO). VERAGUAS: Cerro Tute, E slopes, 1 km beyond Escuela Agricola Alto Piedra above Santa Fé, 900–1,200 m, 14 May 1981, *Sytsma & Andersson 4644* (MO). VENEZUELA. MERIDA: Quebrada El Oso, Palmira, Justo Briceno, 1,600 m, 3–11 Oct. 1973, *López-Palacios & Bautista-Bautista 3481* (MO). COLOMBIA. ANTIOQUIA: between Río Guapa & Río León, 1,000 m, 18 Mar. 1948, *Ruíz Landa et al. 118* (US); 4 km from Palmitas, 1,700 m, 5 Mar. 1949, *Skolnik et al. 19An168* (F, US); road between Yarumal & Valdívia, region of Ventanas, (*Gutierrez et al.*) *Valdivia 5* (US); road between Curamonta & Valparaíso, (*Travecedo & Gouzy*) *Valparaiso 3* (US). CAUCA: Popayán, Timbio in Hato-Viejo, 1,800 m, 14 July 1939, *Cuatrecasas & Pérez-Arbeláez 6070* (F, US); Cordillera Occidental, E slope, Cuchilla de Tambo, 1,750 m, 23 Aug. 1949, *Idrobo & Fernandez 246* (US); "La Gallera" Micay valley, near Río Joaquim, Cordillera Occidental, 1,400–1,500 m, 29–30 June 1922, *Killip 7846* (NY); Popayán, 1,500–2,000 m, Jan.–Mar., *Lehmann 4770* (F, US) (type of *S. chamaecerasus*). CUNDINAMARCA: Anolaima, 14 Jan. 1954, *David 4852* (US); Santana station, above Sasaima, 160–1,700 m, 25–29 July 1945, *Dugand & Jaramillo 3877* (US); Cordillera Oriental, Finca, "Alto Oscar" 11 km S of La Palma, 5,600 ft., 10 Mar. 1944, *Little 7388* (NY, US). HUILA: Finca Cedral, Quebrada Urraca, Río Fortalecillas above Vega Larga, 30 km E of Neiva, 1,300 m, 2°58′N, 74°58′W, 18 Jan. 1943, *Fosberg 19765* (NY, US). SANTANDER: Río Suratá valley above Suratá, 2,000–2,500 m, 5–6 Jan. 1927, *Killip & Smith 16531* (NY, US); vicinity of Charta, 2,000–2,600 m, 1–11 Feb. 1927, *Killip & Smith 19089* (NY, US); vicinity of Tona, 1,900–2,100 m, 17 Feb. 1927, *Killip & Smith 19505* (NY, US). TOLIMA: El Líbano above San José, 1,580–1,620 m, 19 July 1947, *García-Barriga 12239* (US). VALLE DE CAUCA: Cordillera Occidental, E slope between Bitaco & Yumbo, 1,700 m, 5 Apr. 1979, *Cuatrecasas & Cuadros 28837* (US); Río Nima above Tenjo, 1,850 m, 2 Oct. 1974, *Maas & Plowman 1827* (MO). ECUADOR. LOJA: Km 25, Loja to San Lucas, 2,200 m, 15 Sept. 1961, *Dodson & Thien 635* (MO, US). PERU. sin. loc. 1840, *Mathews 3249* (NY). AMAZONAS: Bongará, Jalca zone 3 km S of Pomacocha, E of Shipasbamba trail, 2,400 m, 20 June 1962, *Wurdack 997* (US). AYACUCHO: La Mar, ca. 25 km walking distance SW of Hacienda Luisana & Río Apurímac, ca. 12 km from Hacienda Santa Rosa, ca. 25 km from Tambo, E massif of Cordillera Central, 1,570 m, 12°43′S, 73°50′W, 20 Aug. 1968, *Dudley 11879* (F); Ccarrapa between Huanta & Río Apurímac, 2,200 m, 5, 6, 17 May 1929, *Killip & Smith 2306* (NY); La Mar, just below Huanhuachayo on the Capprichio–Puncu trail, W slope of Río Apurímac valley, 1,590 m, 12°43′S, 73°47′W, 15 July 1970, *Madison 10265–70* (F). CUZCO: "Pillahuata" Cerro de Cusilluyoc, 2,400–2,500 m, 3–6 May 1925, *Pennell 13951* (F, NY). HUÁNUCO: Pachitea, Panao, 2,700–2,900 m, 3 Mar. 1947, *Ferreyra 1766* (US, USM); Huacachi, station near Muña, 6,500 ft., 20 May–1 June 1923, *Macbride 4155* (F); road from Huánuco to Tingo María N of Carpish Pass, 54 km NE of Huanuco, 2,310 m, 6 Dec. 1981, *Plowman & Rury 11164A* (F). JUNÍN: Tarma, at little bridge on Tarma–San Ramon road, 1 km above Matichacra, just below Carpupata, E side of Río Tarma valley opposite mouth of Río Huasihuasi, 11 km NNE of Palca, 2,000 m, 4 Dec. 1962, *Iltis et al. 322* (US, WIS); Pichís trail, between Yapas & Eneñas, 1,800 m, 28 June–8 July 1929, *Killip & Smith 25618* (US); Schunke hacienda above San Ramón, 1,300–1,700 m, Aug.–Oct. 1923, *Schunke A101* (US); Chancamayo valley, 1,500 m, Nov. 1925–1927, *Schunke 258* (F). PUNO: Sandía, Santo Domingo, 1,550 m, 4 Nov. 1939, *McCarroll 52* (NY). BOLIVIA. LA PAZ: S Yungas, basin of Río Bopi, San Bartolome (near Calisaya), 750–900 m, 1–22 July 1939, *Kruckoff 10452* (F, MO, NY, US). SANTA CRUZ: Río Piraymiri, Valle Grande, 2,900 m, Feb. 1956, *Cardenas 5118* (US).

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POLLEN MORPHOLOGY OF THE GENUS *ERYTHRINA* (LEGUMINOSAE: PAPILIONOIDEAE) IN RELATION TO FLORAL STRUCTURE AND POLLINATORS[1]

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ABSTRACT

The unacetolysed pollen of 99 species of *Erythrina* was studied with scanning electron microscopy. The exine sculpturing is basically reticulate but displays considerable variation in several features. Pollen types may be divided into those species with tubular, hummingbird-pollinated flowers and those with gaping flowers, pollinated by a variety of passerine birds. "Hummingbird type" pollen may be defined as medium-sized, with medium-sized lumina and sparse or no sexinous granules. Pollen from passerine-pollinated sections is more heterogeneous but may be distinguished generally by moderate to dense granularity or small lumina size. Some overlap occurs between these groups. Pollen from some passerine-pollinated sections frequently showed an abundance of pollenkitt, which was sparse or lacking in hummingbird groups. These observations are discussed and possible explanations suggested.

Palynological contributions to taxonomy, in disclosing and suggesting relationships between taxa, have emerged hitherto principally from comparative study of structure and ornamentation among pollen. Recently, however, attention has become focused increasingly on functional aspects of the structural details observed. The maintenance of pollen in a viable state, its transfer to a stigma, and successful germination on a compatible stigma are essential to normal sexual reproduction in flowering plants. Under constant environmental pressures many features of pollen structure and physiology may lead to failure, or conversely promote success, at any stage. Thus, it seems reasonable to expect that pollen, subject to natural selection just as much as the whole plant, has evolved to meet the demands imposed upon it.

However, the situation is unlikely to be simple. A plant is constrained within certain limitations by its basic genetic inheritance. Compromises often must be made between conflicting factors. Nor is it necessarily true that a plant is optimally adapted with respect to all (or any) of its morphological features: for example, an inefficient pollination system may be compensated for by great longevity. Evolutionary processes and environmental conditions are both in a state of continuous chance but not all features are necessarily of any immediately obvious adaptive significance.

In a relatively close-knit genus, such as *Erythrina,* it seems reasonable to assume that the species have radiated relatively recently from an ancestral stock and have preserved a basic similarity in pollen structure and potential for evolutionary change. However, *Erythrina* is also a large genus, widely distributed in both the Old and New Worlds. Although all species are primarily pollinated by birds of one sort or another (Toledo, 1974; Raven, 1979), there seems to be distinct syndromes in floral biology within the genus, apparently associated with pollination strategy. There is considerable variation among species in floral structure and presentation (Krukoff & Barneby, 1974; Lucas & Theobald, 1982) and in behavior and approach of pollinators. As different modes of survival and efficient transference of the pollen develop, morphological modifications of the pollen itself might be ex-

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pected. However, climatic, ecological, or other factors may also influence evolution, and random variation, whether genetically or environmentally induced, may also occur.

Ferguson and Skvarla (1982) have shown that in the subfamily Papilionoideae there is a close association between pollen ornamentation and stratification with flower structure and pollination system, notably in some species with flowers adapted for pollination by birds or bats. This association between pollen morphology and floral structure occurs in species and genera from widely separated tribes, and it is suggested that it is the result of convergent evolution and a secondary adaptation to pollination. The pollen morphology of *Erythrina* was not included in their investigation. Graham and Tomb (1974, 1977) made a detailed study of the pollen of *Erythrina* in relation to taxonomy but without consideration of the approach discussed above. These workers gave an extensive bibliography of the pollen morphology of the genus, which can be supplemented by reference to Thanikaimoni (1976, 1980).

The aim of the present study, using herbarium material, is to examine the links between pollen morphology, flower structure, and pollination ecology.

Materials and Methods

Pollen was obtained primarily from herbarium specimens at the Royal Botanic Gardens, Kew (K). Material was also obtained from the herbarium of the New York Botanical Garden (NY) and the Missouri Botanical Garden (MO). Details of the specimens examined are shown in Table 1. The data presented in Table 1 are based on scanning electron microscope (SEM) micrographs of untreated pollen removed directly from herbarium sheets. This procedure was followed because, although acetolysis (Erdtman, 1969) in most cases somewhat improved the clarity of the ornamentation and increased the size of the pollen grains, it removed the residual pollenkitt found on many unacetolysed pollen. Differences in the occurrence and volume of pollenkitt present in pollen samples were found to be of some significance. This will be discussed later.

The pollen was prepared by removing mature anthers from herbarium sheets and shaking or brushing the pollen onto double-sided sticky tape on SEM specimen stubs. The samples were sputter coated with platinum and examined with a Jeol T20 SEM.

Pollen Morphology

From the 99 species of *Erythrina* examined in this study, and from the results of Graham and Tomb (1974, 1977), the pollen may be described as follows: oblate; rounded-triangular in polar view; ranging in size from 22 to 55 μm diam.; triporate, occasionally tetraporate, pores more or less equally spaced, equatorially arranged at the corners; surface ornamentation basically reticulate, but with considerable variation in the size and shape of the lumina, the height and width of the muri, and the occurrence and prominence of sexinous granules in the lumina. In occasional samples the muri are discontinuous on either the polar or equatorial faces (e.g., *E. dominguezii, E. lysistemon*). Rarely is there little or no organized reticulum, and the ornamentation consists of discontinuous muri or sexinous granules.

Each of the main features of variation in the pollen morphology is discussed briefly in turn and the data for each species are summarized in Table 1.

SIZE AND SHAPE

The pollen diameter of the majority of species falls in the range 23–30 μm, as measured on electron micrographs of unacetolysed material [these sizes are proportionally smaller than those given by Graham and Tomb (1977) for acetolysed pollen].

A few species have pollen that is smaller than average, 20–23 μm diam. These include *E. crista-galli, E. arborescens, E. breviflora, E. edulis, E. suberosa, E. stricta,* and *E. resupinata. Erythrina eggersii* has atypically small pollen among the six sections characterized by tubular, hummingbird pollinated flowers in subgenus *Erythrina,* which otherwise have medium, rarely medium- to large-sized pollen.

Large pollen, 30–35 μm diam., occurs predominantly in subgenus *Erythraster,* in a number of species in subgenus *Chirocalyx,* and in the monotypic section *Acanthocarpae* in subgenus *Erythrina.*

The pollen of *E. fusca* is particularly variable in size. Large, medium, and small pollen are all represented by different samples (see Table 1).

The shape of the pollen of the vast majority of species is rounded-triangular in polar view. However, that of a few sections, i.e., *Suberosae, Arborescentes, Breviflorae, Leptorhizae,* and *Oliviae*—all subgenus *Erythrina,* is markedly triangular, while that of other species (e.g., in subgenus *Erythraster*) is more rounded.

TABLE 1. Specimens examined with details of origin and a summary of the main pollen characters, types, and vectors. The species are arranged in the taxonomic order of Krukoff and Barneby (1974). The data columns are blank opposite a small number of species. These are species where the pollen morphology has not been examined because suitable material was not readily available. Sizes are relative and have been derived from comparable samples.

Species	Collection	Locality	Deposited	Pollen			Lumina		Muri Width[f]	Sexinous Granules[g]
				Size[a]	Type[b]	Vector[c]	Size[d]	Type[e]		
subg. *Micropteryx* (Walpers) J. G. Baker										
sect. *Duchassaingia* (Walpers) Krukoff										
E. fusca Loureiro	*Haniff 348*	Malaya	(K)	m	d	P	m	dis	b	++
	Millar 13818	New Guinea	(K)	l	a	P	vs	r	m	+
	Hildebrandt 1594	Comoro Is.	(K)	s	a	P	vs	r	m	+
	Heyde & Lux s.n.	Guatemala	(K)	m/s	e	P	m/s	dis	m	+
	Irwin 48782	Brazil	(K)	l	c	P	l	dis	m	+
sect. *Cristae-galli* Krukoff										
E. crista-galli L.	*Pedersen 820*	Argentina	(K)	s	a	P	s	s	m	−
E. falcata Benth.	*Venturi 9705*	Argentina	(K)	m/s	c	P	m	r	m	+
sect. *Micropteryx*										
E. dominguezii Hassler	*Venturi 5040*	Argentina	(K)	m	e	P	m	dis	m	++
E. ulei Harms	*Prance 23714*	Peru	(K)	m	e	P	l	dis	m	+
E. verna Velloso	*Burchell 818-2*	Brazil	(K)	m	c	P	m	r	b	+
E. poeppigiana (Walpers) O. F. Cook	*Fendler 308*	Venezuela	(K)	m	b	P	m	r	m	+
	Schultes et al. 5100	Colombia	(K)	m	b	P	m	r	m	+
subg. *Erythrina*										
sect. *Suberosae* Krukoff										
E. suberosa Roxb.	*Hooker 77*	India	(K)	s	a	P	s	±dis	n	++
E. microcarpa Koorders & Valeton	*Backer s.n.*	Java (cult.)	(K)	m	a	P	s	s	m	+
E. stricta Roxb.	*Bullock 975*	India	(K)	s	a	P	m/s	s	m	+
E. resupinata Roxb.	*Clarke 34732*	India	(K)	s	e	P	m/s	dis	n/m	+
	Mooney 762	India	(K)	s	a	P	s	s	m	±
sect. *Arborescentes* Krukoff										
E. arborescens Roxb.	*Clarke 26834E*	India	(K)	s	a	P	s	sr	n	−

TABLE 1. Continued.

Species	Collection	Locality	Deposited	Pollen			Lumina		Muri Width[f]	Sexinous Granules[g]
				Size[a]	Type[b]	Vector[c]	Size[d]	Type[e]		
sect. *Hypaphorus* (Hassk.) Krukoff										
E. subumbrans (Hassk.) Merrill	*Sørensen et al. 1708*	Thailand	(K)	m	c	P	s	sr	m	++
	Merrill 1950	Philippines	(K)	m	c	P	s	sr	m	++
sect. *Breviflorae* Krukoff										
E. breviflora DC.	*McVaugh 13210*	Mexico	(K)	s	a	P	vs	sr	m	–
	McVaugh 13582	Mexico	(K)	s	a	P	vs	sr	m	–
E. batolobium Barneby & Krukoff	*Neill 5650*	Mexico	(MO)	m	a	H	s	sr	n	–
sect. *Edules* Krukoff										
E. edulis Triana	*MacBryde 694*	Ecuador	(K)	s	a	P	s	sr	n	–
sect. *Stenotropis* (Hassk.) Krukoff										
E. speciosa Andrews	*Retitz & Klein s.n.*	Brazil	(K)	m	a/b	H	s	s	m	+
sect. *Pseudo-edules* Krukoff & Barneby										
E. polychaeta Harms	–	–	–	–	–	–	–	–	–	–
E. schimpffii Diels	*Camp E. 3643*	Ecuador	(K)	m	a/b	H	s	sr	m	±
sect. *Leptorhizae* Krukoff										
E. montana Rose & Standley	*Palmer 450*	Mexico	(K)	m	b	H	s	sr	n	–
E. leptorhiza DC.	*Balls & Gourlay B4826*	Mexico	(K)	l	b	H	m/s	r	n	–
E. horrida DC.	*Pringle 4687*	Mexico	(K)	m	a	H	vs	r	n	–
sect. *Erythrina*										
E. herbacea ssp. *nigrorosea* Krukoff & Barneby	*Rovirosa 696*	Mexico	(K)	m/s	b	H	m	sr	m	–
E. standleyana Krukoff	*Krukoff 1970-77*	Mexico	(K)	m	b	H	m	r	m	–
E. flabelliformis Kearney	*Gentry 2202*	Mexico	(K)	m	b	H	m	r	m	–
E. coralloides DC.	*Krukoff 128*	Mexico	(K)	m	b	H	l	sr	m	–
	Krukoff 1970-124	Mexico	(K)	m	b	H	l	sr	m	+
E. aff. *coralloides* DC.	*Krukoff 1970-130*	Mexico	(NY)	m	b	H	m	r	m	±
E. pudica Krukoff & Barneby	*Krukoff 1970-79*	Mexico	(NY)	m	b	H	m	±r	n	±

TABLE 1. Continued.

Species	Collection	Locality	Deposited	Pollen			Lumina		Muri Width[f]	Sexinous Granules[g]
				Size[a]	Type[b]	Vector[c]	Size[d]	Type[e]		
E. lanata ssp. *lanata* Rose	*Hinton 10030*	Mexico	(K)	m	b	H	m	sr	m	±
E. lanata ssp. *occidentalis* Standley	*Stork et al. 25186*	Mexico	(K)	m	b	H	m	r	m	−
E. goldmanii Standley	*Krukoff 1970-77*	Mexico	(K)	m	b	H	m	±dis	m	−
E. caribaea Krukoff & Barneby	*Krukoff 1970-95*	Mexico	(K)	m	b	H	l	r	m	±
E. folkersii Krukoff & Moldenke	*Krukoff 1970-97*	Mexico	(K)	m	b	H	m	sr	m	−
E. tuxtlana Krukoff & Barneby	*González 0.2211*	Mexico	(NY)	m	b	H	m	sr	m	−
E. smithiana Krukoff	*MacBryde 946*	Ecuador	(K)	m	b	H	m	sr	m	−
E. cochleata Standley	*Neill 5102*	Costa Rica	(NY)	m/l	b	H	m	sr	m	±
E. hondurensis Standley	*Saunders 1012*	Honduras	(NY)	m/l	e	H	m	dis	b	−
				m/l	b	H	m	s	b	−
E. chiapasana Krukoff & Barneby	*Krukoff 1969-215*	Guatemala	(K)	m/l	b	H	m	r	n/m	−
E. atitlanensis Krukoff & Barneby	*Krukoff 1969-175*	Guatemala	(K)	m	b	H	m	s	b	±
E. cobanensis Krukoff & Barneby	*Krukoff 1970-11*	Guatemala	(K)	m	b	H	m	sr	n	−
E. williamsii Krukoff & Barneby	*Williams 40260*	Guatemala	(NY)	m	b	H	m	sr	n/m	±
E. tajumulcensis Krukoff & Barneby	*Krukoff 1970-62*	Mexico	(K)	m	b	H	m	sr	n/m	−
E. chiriquensis Krukoff	*Croat 10497*	Panama	(NY)	m	b	H	m	sr	n/m	−
E. macrophylla DC.	*Krukoff 1969-4*	Guatemala	(K)	m	b	H	m	sr	m	±
E. guatemalensis Krukoff	*Krukoff 1969-31*	Guatemala	(K)	m	b	H	m	sr	n/m	−
E. globocalyx Porsch & Cufod.	*Krukoff 1969-141*	Costa Rica	(K)	m	b	H	m	sr	m	±
E. steyermarkii Krukoff & Barneby	*Stevens 6023*	Nicaragua	(NY)	m	b	H	m	r	m	−
E. florenciae Krukoff & Barneby	*Krukoff 1971-2*	Guatemala	(K)	m	b	H	m	sr	n/m	±
E. berenices Krukoff & Barneby	*Gómez-Pompov 1837*	Mexico	(NY)	m	b	H	m	r	m	−
E. huehuetenangensis Krukoff & Barneby	*Krukoff 1972-8*	Guatemala	(K)	m	b	H	m	s	n/m	−
E. lanceolata Standley	*Edwards 671*	Honduras	(K)	m	b	H	m	sr	n/m	−
E. costaricensis Micheli	*McKee 11114*	Costa Rica	(K)	m	b	H	m	r	n	−
E. barqueroana Krukoff & Barneby	*Krukoff 1972-5*	Guatemala	(K)	m	b	H	m	sr	m	−

TABLE 1. Continued.

Species	Collection	Locality	Deposited	Pollen			Lumina		Muri Width[f]	Sexinous Granules[g]
				Size[a]	Type[b]	Vector[c]	Size[d]	Type[e]		
E. americana Miller	*Fleur s.n.*	Mexico	(K)	m	b	H	m	sr	n/m	–
E. berteroana Urban	*Krukoff 1969-101*	Costa Rica	(K)	m	b	H	m	r	m	–
E. rubrinervia H.B.K.	*Krukoff 1282*	Venezuela	(K)	m	b	H	m	r	m	±
E. mexicana Krukoff	*Langlassé 676*	Mexico	(K)	m/l	b	H	m	s	m	–
E. salviiflora Krukoff & Barneby	*Krukoff 1969-57*	Guatemala	(K)	m	b	H	m	s	m	±
E. castillejiflora Krukoff & Barneby	*Krukoff 1969-233*	Guatemala	(K)	m	b	H	m	s	n/m	–
sect. *Gibbosae* Krukoff & Barneby										
E. gibbosa Cufod.	*Siebert 364*	Panama	(K)	m	b	H	m	r	m	–
sect. *Corallodendra* Krukoff										
E. amazonica Krukoff	*MacBryde 1518*	Ecuador	(K)	m	b	H	m	r	n/m	–
E. similis Krukoff	*Kuntze s.n.*	Bolivia	(NY)	m	b	H	m	s	n/m	–
E. peruviana Krukoff	*Asplund 19524*	Ecuador	(NY)	m	b	H	m	s	n/m	–
E. mitis Jacquin	*Fendler 304*	Venezuela	(K)	m	b	H	m	s	m	–
E. pallida Britton & Rose	*Richards s.n.*	Trinidad	(K)	m	c	H	m	sr	n/m	+
	Broadway 5614	Trinidad	(K)	m	c	H	m	sr	n/m	+
E. corallodendrum L.	*Hahn 721*	St. Vincent	(K)	m	c	H	m	sr	n/m	+
E. eggersii Krukoff & Moldenke	*Britton & Britton 9501*	Puerto Rico	(NY)	s	b	H	m	sr	n/m	±
E. buchii Urban	*Holdridge 947*	Haiti	(NY)	m	b	H	m	r	n/m	–
E. leptopoda Urban & Ekman	*Ekman s.n.*	Haiti	(K)	m	b	H	m	s	n/m	–
E. elenae Howard & Briggs	–	–	–	–	–	–	–	–	–	–
sect. *Cubenses* Krukoff										
E. cubensis C. Wright	*Britton & Cowell 9885*	Cuba	(K)	m	b	?	m	r	m	–
sect. *Olivianae* Krukoff & Barneby										
E. oliviae Krukoff	*Hernandez 2*	Mexico	(NY)	m	a	P	m/s	s	n/m	–
sect. *Caffrae* Barneby & Krukoff										
E. caffra Thunb.	*Codd 7988*	S. Africa	(K)	m	b	P	m	sr	m	±
E. lysistemon Hutch.	*Chase 880*	Zimbabwe	(K)	m	b	P	m	s	m	±
	Methuen 156	Zimbabwe	(K)	m	e	P	m	sr	m	+

TABLE 1. Continued.

Species	Collection	Locality	Deposited	Pollen Size[a]	Pollen Type[b]	Pollen Vector[c]	Lumina Size[d]	Lumina Type[e]	Muri Width[f]	Sexinous Granules[g]
sect. *Humeanae* Barneby & Krukoff										
E. humeana Spreng.	*Codd 9297*	S. Africa	(K)	m	b	P	m	sr	m	±
	Whellan 2217	Mozambique	(K)	m	b	P	m	sr	m	±
E. zeyheri Harvey	*Rogers 14814*	S. Africa	(K)	m	a	P	vs	s	n/m	±
	Holub s.n.	S. Africa	(K)	m	a/b	P	m	r	m/b	±
sect. *Acanthocarpae* Barneby & Krukoff										
E. acanthocarpa E. Meyer	*Tysm s.n.*	S. Africa	(K)	l	c	P	m	sr	m	+
subg. *Tripterolobus* Barneby & Krukoff										
sect. *Tripterolobus*										
E. greenwayi Verdc.	—	—	—	—	—	—	—	—	—	—
subg. *Chirocalyx* (Meisner) Harvey										
sect. *Bruceanae* Barneby & Krukoff										
E. brucei Schweinf.	*Mooney 8873*	Ethiopia	(K)	l	c	P	m	sr	m	++
sect. *Macrocymbium* (Walpers) Barneby & Krukoff										
E. vogelii Hook. f.	*Moloney s.n.*	Nigeria	(K)	m/l	d	P	l	dis	b	++
E. senegalensis DC.	*York 85*	Sierra Leone	(K)	m	c	P	m	sr	b	+
sect. *Dilobochilus* Harms										
E. excelsa Baker	*Snowden 1878*	Uganda	(K)	m/l	c	P	m	s	b	+
sect. *Dichilocraspedon* Harms										
E. mildbraedii Harms	*Deighton 3884*	Sierra Leone	(K)	m	c	P	m/s	s	m	+
sect. *Chirocalyx*										
E. pygmaea Torre	—	—	—	—	—	—	—	—	—	—
E. mendesii Torre	*Drummond & Cookson 6225*	Zambia	(K)	m	c	P	m	sr	b	+
E. baumii Harms	—	—	—	—	—	—	—	—	—	—
E. decora Harms	*Seydel 369*	S.W. Africa	(K)	m	c	P	m	sr	m	+
E. livingstoniana Baker	*Phelps 283*	Zimbabwe	(K)	l	b	P	m	sr	m	±
E. tholloniana Hua	—	—	—	—	—	—	—	—	—	—
E. addisoniae Hutch.	*Vigne 1183*	Ghana	(K)	m	a	P	vs	sr	b	±
E. droogmansiana Wildem. & Durand	*Feux 5070*	Cameroon	(K)	m/l	c	P	s	sr	m	+

TABLE 1. Continued.

Species	Collection	Locality	Deposited	Pollen			Lumina		Muri Width[f]	Sexinous Granules[g]
				Size[a]	Type[b]	Vector[c]	Size[d]	Type[e]		
E. orophila Ghesquiere	*Ghesquière 5030*	Zaire	(K)	m/l	c	P	m	s	m	+
E. sacleuxii Hua	*Greenway 4849*	Tanzania	(K)	l	d	P	l	s	m	++
E. haerdii Verdc.	*Culwick s.n.*	Tanzania	(K)	m	b	P	m	sr	m	±
E. sigmoidea Hua	*Sanford 6230*	Cameroon	(K)	s	c	P	m	s	m	+
E. latissima E. Meyer	*Plowes 1264*	Zimbabwe	(K)	l	d	P	l	s	b	++
E. abyssinica Lam.	*Ringoet 39*	Zaire	(K)	m	c	P	s	r	m	+
	Hornby 926	Tanzania	(K)	m	c	P	s	sr	m	+
subg. *Erythraster* Barneby & Krukoff										
sect. *Erythraster*										
E. variegata L.	*Robinson 533*	Sumatra	(K)	l	d	P	l	sr	b	++
	Kerr 14233	Thailand	(K)	l	d	P	l	sr	b	++
	Rudd 3096	Sri Lanka	(K)	l	d	P	l	sr	b	++
	Last s.n.	Tanzania	(K)	l	d	P	m	sr	b	++
	Schodde 2743	New Guinea	(K)	m		P	surface finely granular/smooth			
E. tahitensis Nadeau	*Brenan 14902A*	Hawaii	(K)	l	f	P	s–l	r	b	+
E. euodiphylla Hassk.	*Jacobs 4886*	Java	(K)	l	d	P	s	r	b	+
E. vespertilio Benth.	*Scarth Johnson 539*	Australia	(K)	l	d	P	m/l	sr	b	+
E. vespertilio Benth. (island form)	*Hyland 8955*	Australia	(K)	m	d?	P	m	sr	b	+
E. merrilliana Krukoff	*Schodde 2642*	New Guinea	(K)	l	f	P	s–l	r	b	+
E. velutina Willd.	*Hanbury Tracy 287*	Colombia	(K)	l	d	P	l	sr	b	++
E. grisebachii Urban	*Wright 2347*	Cuba	(K)	l	d	P	s/m	sr	b	±
E. burttii Baker f.	*Greenway 9579*	Kenya	(K)	l	d	P	m	dis	b	+
E. burana Chiov.	*Burger 1435*	Ethiopia	(K)	l	d	P	s	dis	b	–
	Haimanot s.n.	Ethiopia	(K)	l	d	P	m/l	sr	b	±
E. perriori Viguier	–	–	–	–	–	–	–	–	–	–
E. schliebenii Harms	–	–	–	–	–	–	–	–	–	–
E. melanacantha Taub.	*Newbould 3586*	Kenya	(K)	l	d	P	sm	s	b	±

[a] Pollen size: s = small, m = medium, l = large.
[b] Pollen type: see text.
[c] Pollen vector: P = passerine birds, H = hummingbirds.
[d] Lumina size: vs = very small, s = small, m = medium, l = large.
[e] Lumina type: r = round, s = sinuous, sr = sinuous and round, dis = discontinuous (where lumina merge together due to breaks in the muri).
[f] Muri width: n = narrow, m = medium, b = broad.
[g] Occurrence and relative prominence/density of sexinous granules: – = absent, ± = very sparse, + = present (may sometimes be quite dense but in low relief), ++ = very dense or large and prominent in high relief.

ORNAMENTATION

SHAPE AND SIZE OF LUMINA

The average width of the lumina varies from extremely narrow, ca. 1 μm, to much broader, ca. 6–8 μm, but with typical values in the range 1–3 μm. The shape of the lumina varies from distinctly sinuous to more rounded in outline but with numerous intermediate categories. Furthermore, the reticulum may be more or less closed, or the muri may have frequent free ends, making the reticulum discontinuous and irregular.

On the whole, these characteristics do not correlate readily with taxonomic groupings in the genus or with each other. Thus, in all four main subgenera, and indeed some of the larger sections, large, medium, and small lumina size are all represented, and each may be associated with sinuous, rounded, or intermediate lumina shape (e.g., compare Figs. 25–27, all sect. *Chirocalyx*, or Figs. 28–30, all sect. *Erythraster*). Isolated instances of pollen showing a discontinuous reticulum occur sporadically throughout the subgenera and sections.

The largest section in the genus, *Erythrina*, is also the most consistent with regard to lumina size, nearly all species in this section having pollen with medium-sized lumina. This is true also of the closely related sections *Corallodendra* and *Gibbosae*. However, within this group of species characterized by tubular, "hummingbird flowers," the small sections *Leptorhizae*, *Pseudoedules*, and *Stenotropis* are somewhat anomalous, having pollen with markedly smaller lumina (Figs. 19, 20). Among the passerine-pollinated species, several small sections contain species that also have pollen with predominantly medium-sized lumina (e.g., *Micropteryx*, *Caffrae*, *Humeanae*). Other sections are marked by pollen with much smaller lumina [*Suberosae*, *Arborescentes*, *Hypaphorus*, *Breviflorae*, *Edules*, and *Oliviae* (see Figs. 7–12)].

A particularly distinct patterning, in which very small round lumina occur on polar faces, opening out to much broader lumina and more discontinuous muri on equatorial faces, is found in only two species, *E. tahitensis* and *E. merrilliana*, both in sect. *Erythraster*.

Erythrina fusca was found once again to be very variable with respect to lumina size (Figs. 1, 2).

APPEARANCE AND SIZE OF THE MURI

Differences in the size and general appearance of the muri occur. The muri are usually of moderate relief and width (ca. 1 μm high and 1 μm wide), somewhat rough and ridged in appearance on the sides and fairly smooth and domed on top. Also the sides of the muri may sometimes be more or less smooth (see Figs. 14, 16, 18). This is found in the majority of species.

Particularly broad, flat-topped muri occur in some species of subgenus *Erythraster* [e.g., *E. variegata* (Fig. 36) and *E. velutina*]. However, in other species of the subgenus the muri are of high relief and are irregularly ridged (e.g., *E. grisebachii*).

A number of species in subgenus *Chirocalyx*, and also *E. zeyheri*, have very smooth muri supported by long columellae that are higher than the sexinous granules in the lumina and give the ornamentation a characteristic rather raised appearance (e.g., see Figs. 23, 25).

In *E. poeppigiana* and *E. cubensis*, the muri are fairly broad and in low relief.

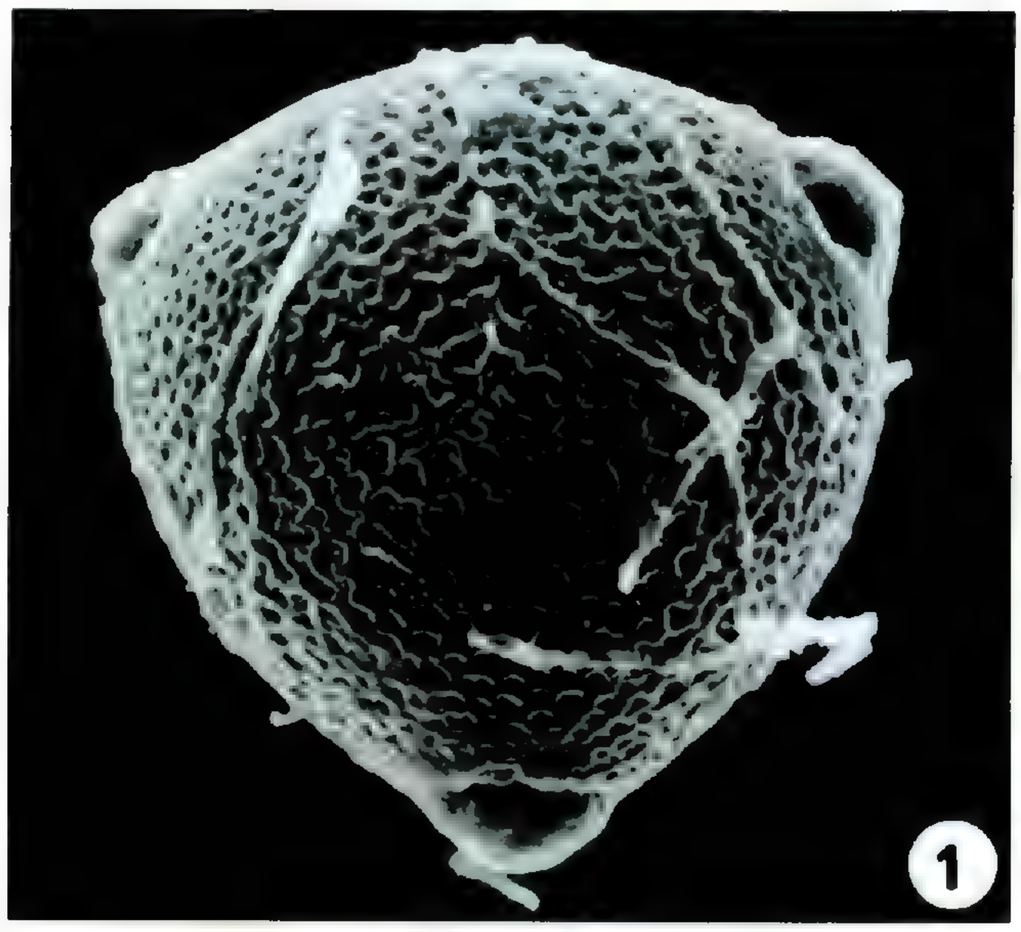
Species of section *Suberosae* (*E. microcarpa*, *E. stricta*, and *E. resupinata*) have flattened, square-topped muri that give an impression of regular segmentation along their length (Fig. 4).

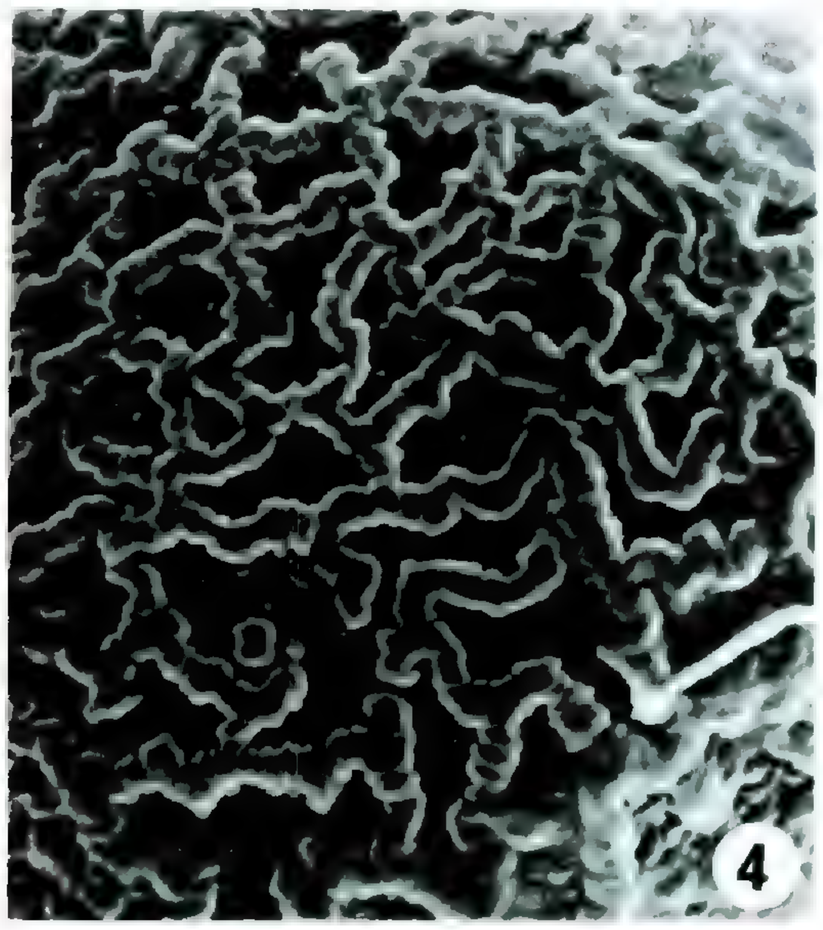
SEXINOUS GRANULES

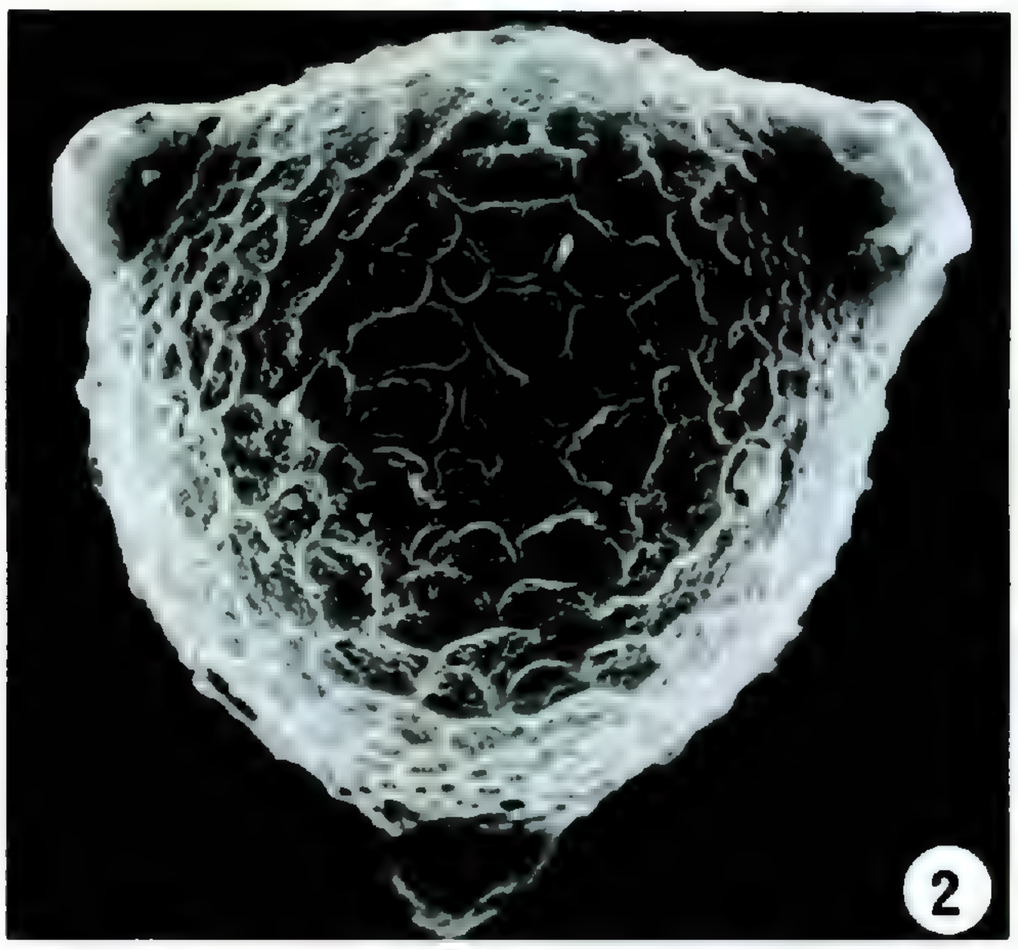
The sexinous granules in the lumina of the reticulum show a complete range from virtually absent or of very low relief to extremely prominent and numerous.

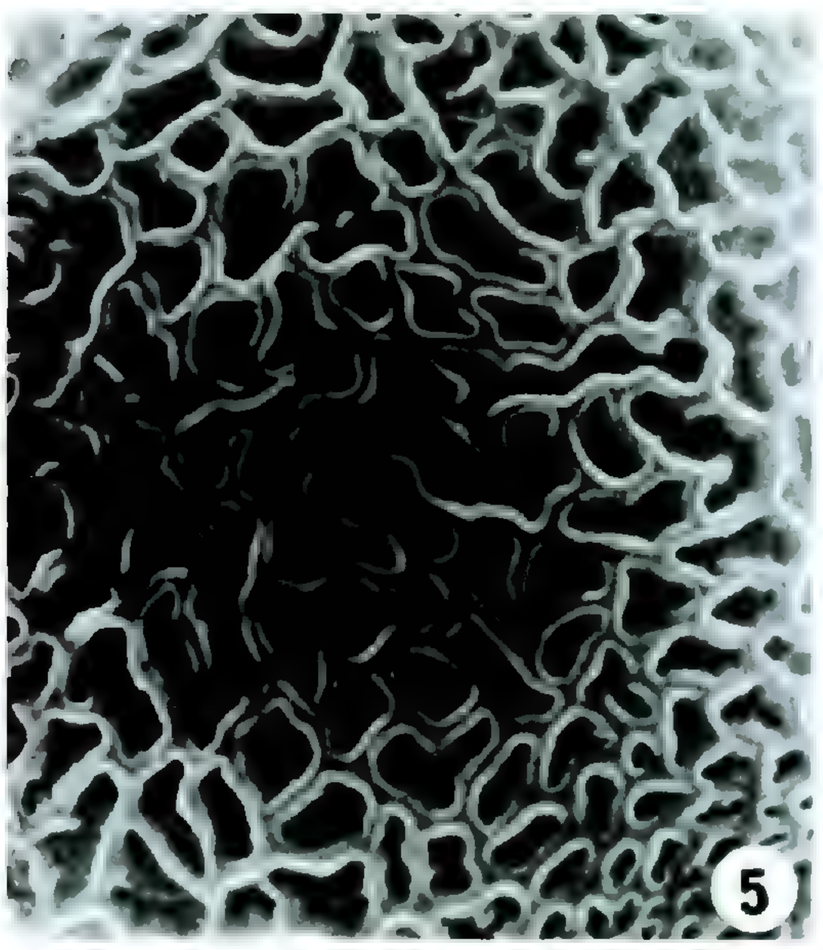
Four of the five specimens of *E. variegata* examined showed the most prominent sexinous granules, these occupying most of the area within the large lumina, and of roughly the same height as the broad muri (Fig. 36). Anomalous in this respect was one sample of *E. variegata* (*Schodde 2743*) from New Guinea, which had no reticulate patterning on any of its pollen and an almost completely smooth appearance (Ferguson & Skvarla, 1981); this specimen needs further investigation.

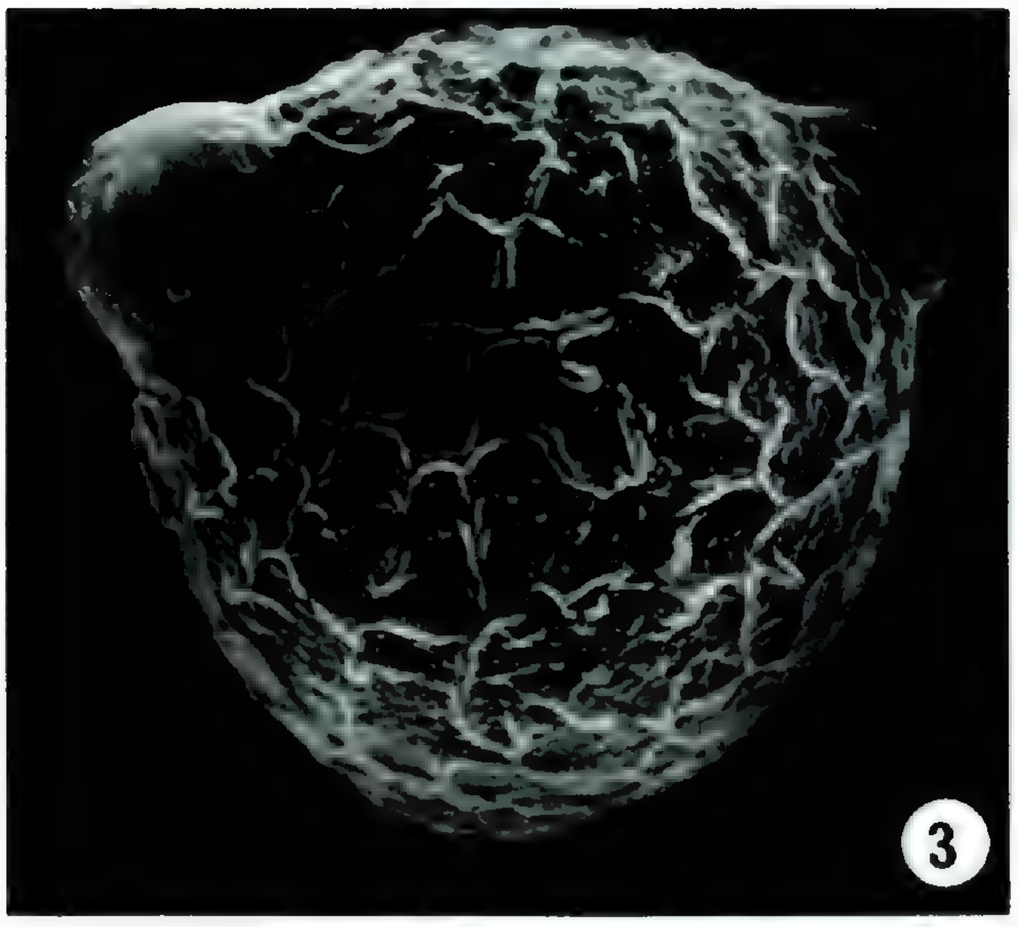
A number of other species, mainly in the subgenera *Chirocalyx* and *Erythraster*, but also including *E. fusca* (*Haniff 348*; Fig. 2) and *E. dominguezii*, have particularly dense and prominent granules. By contrast, sexinous granules are absent, or sparse and low, in virtually all species within the six sections characterized by tubular,

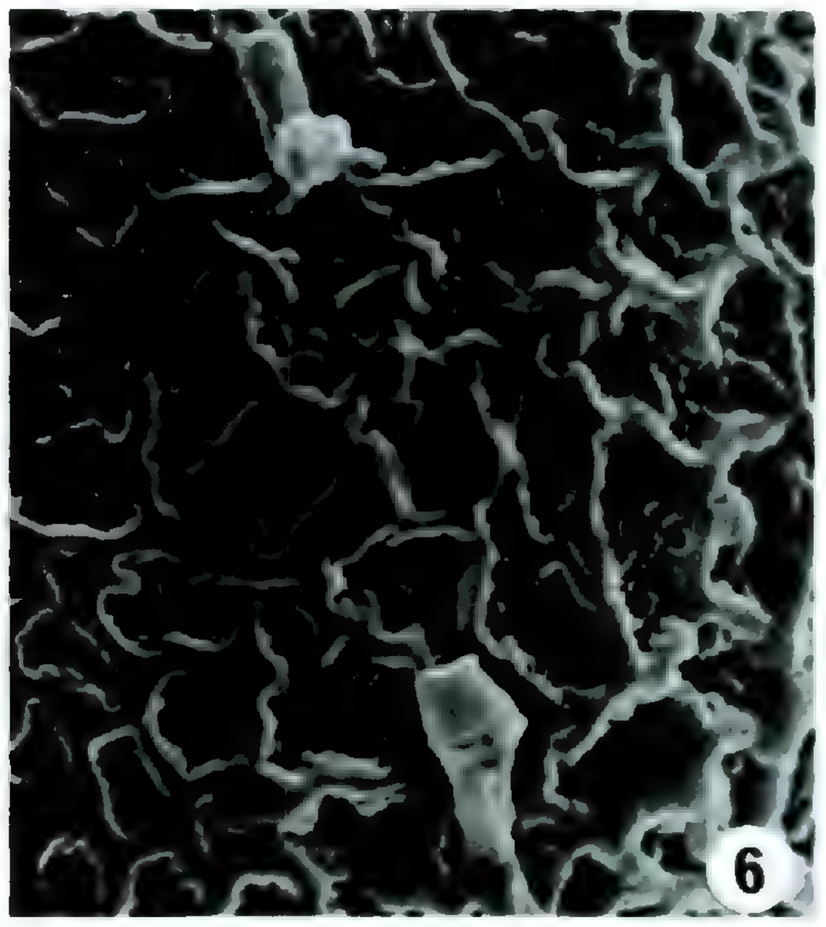




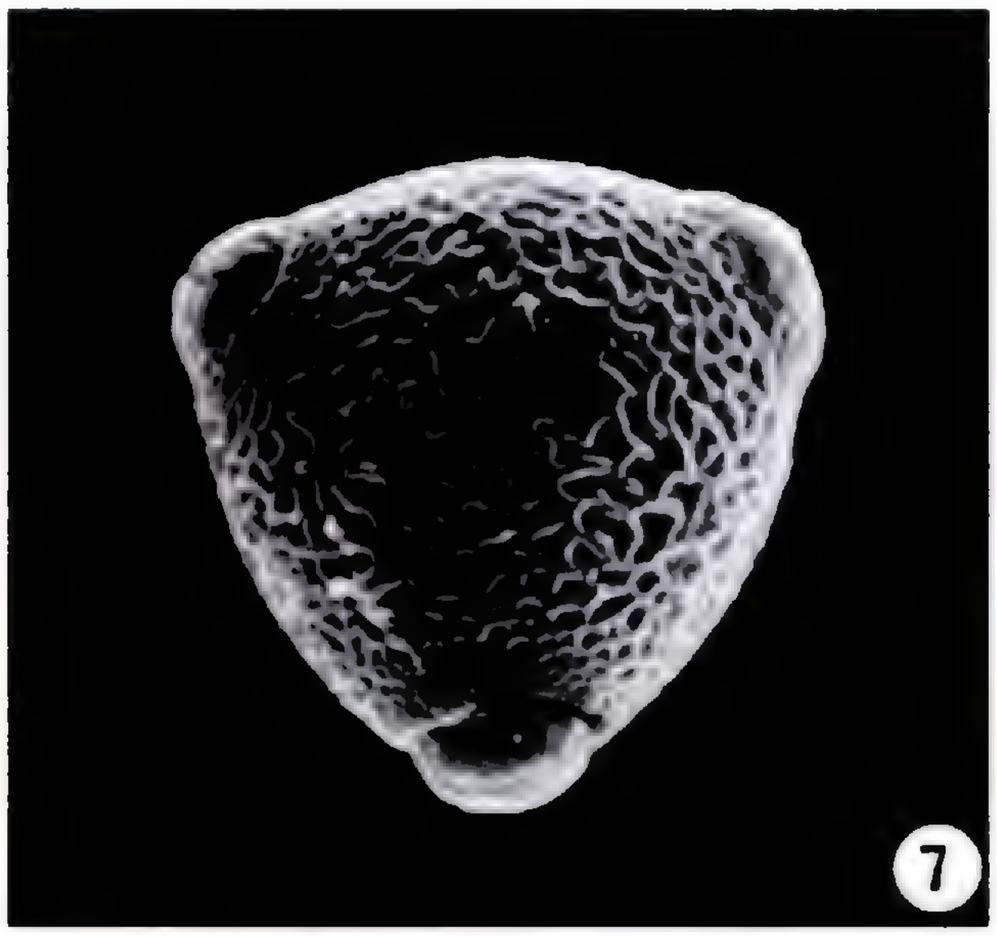


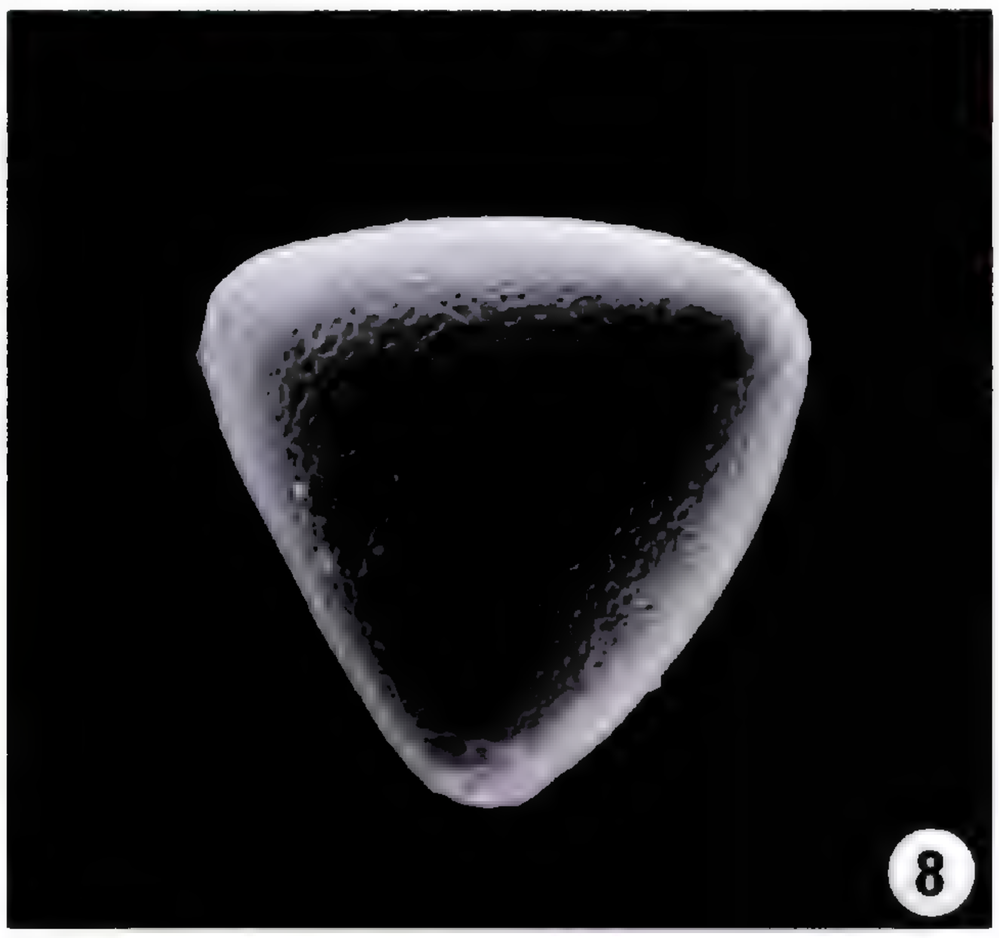


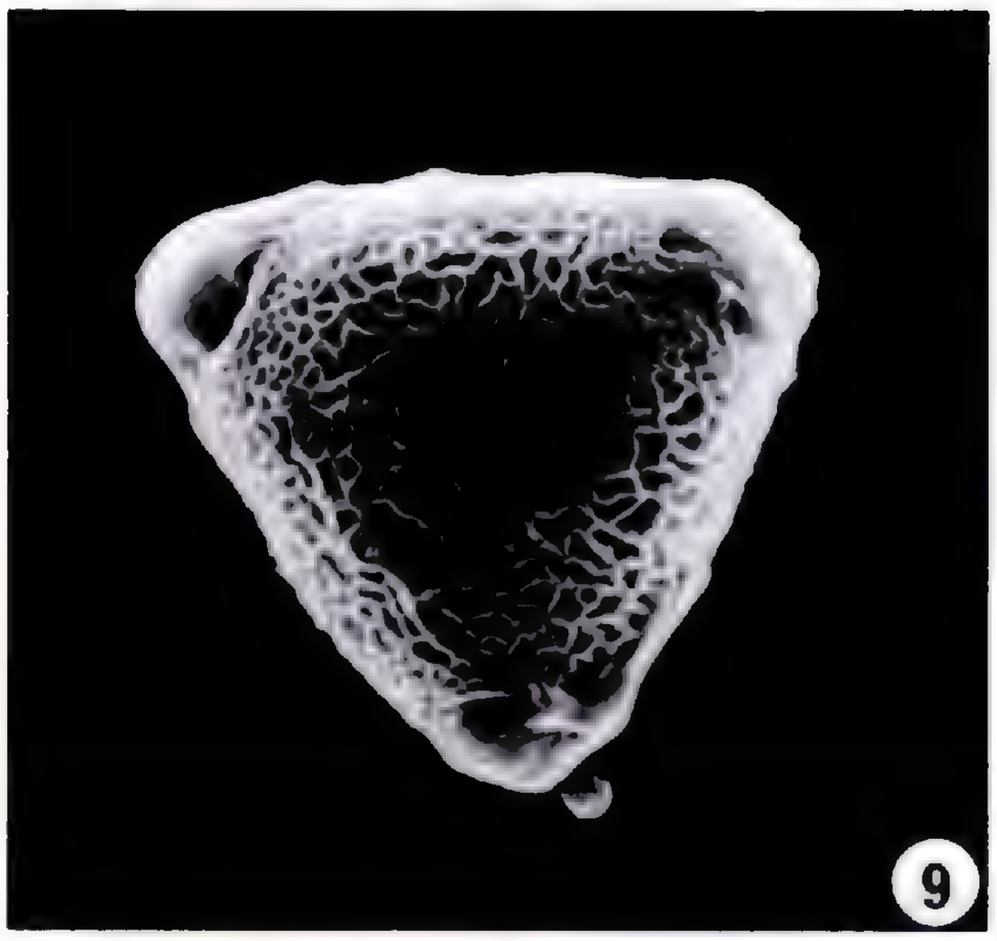


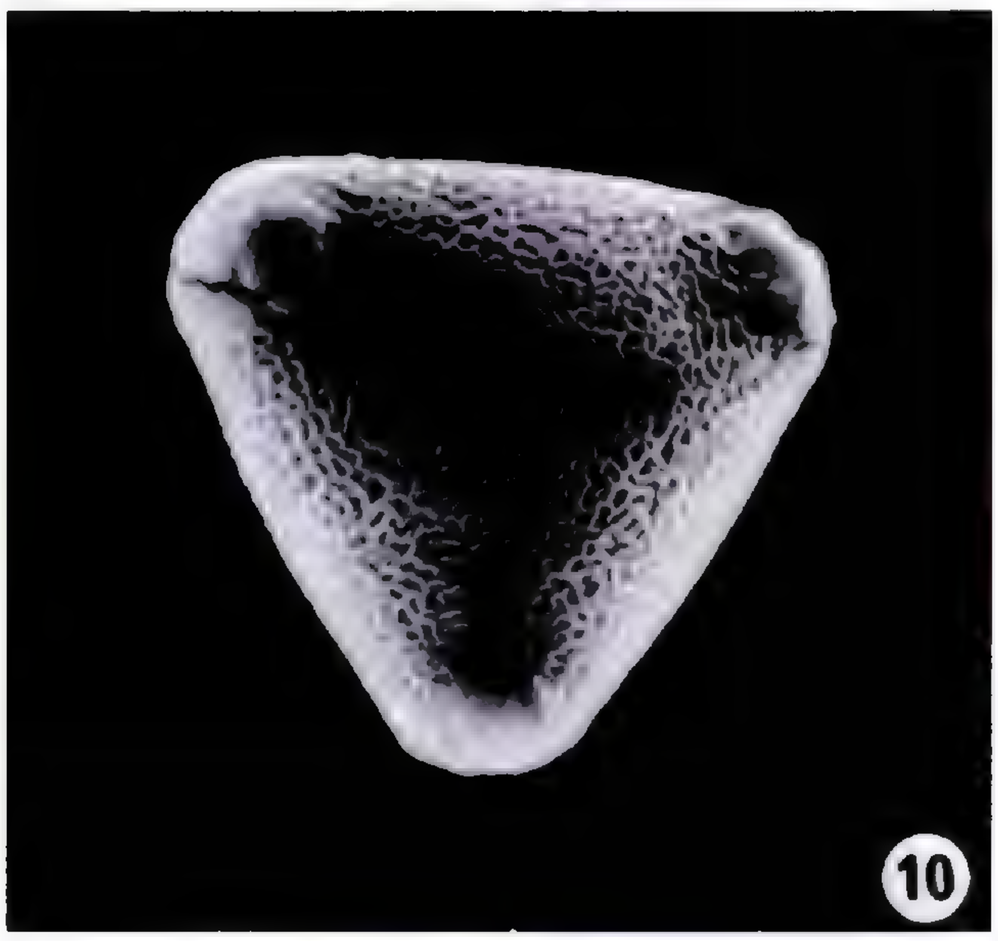


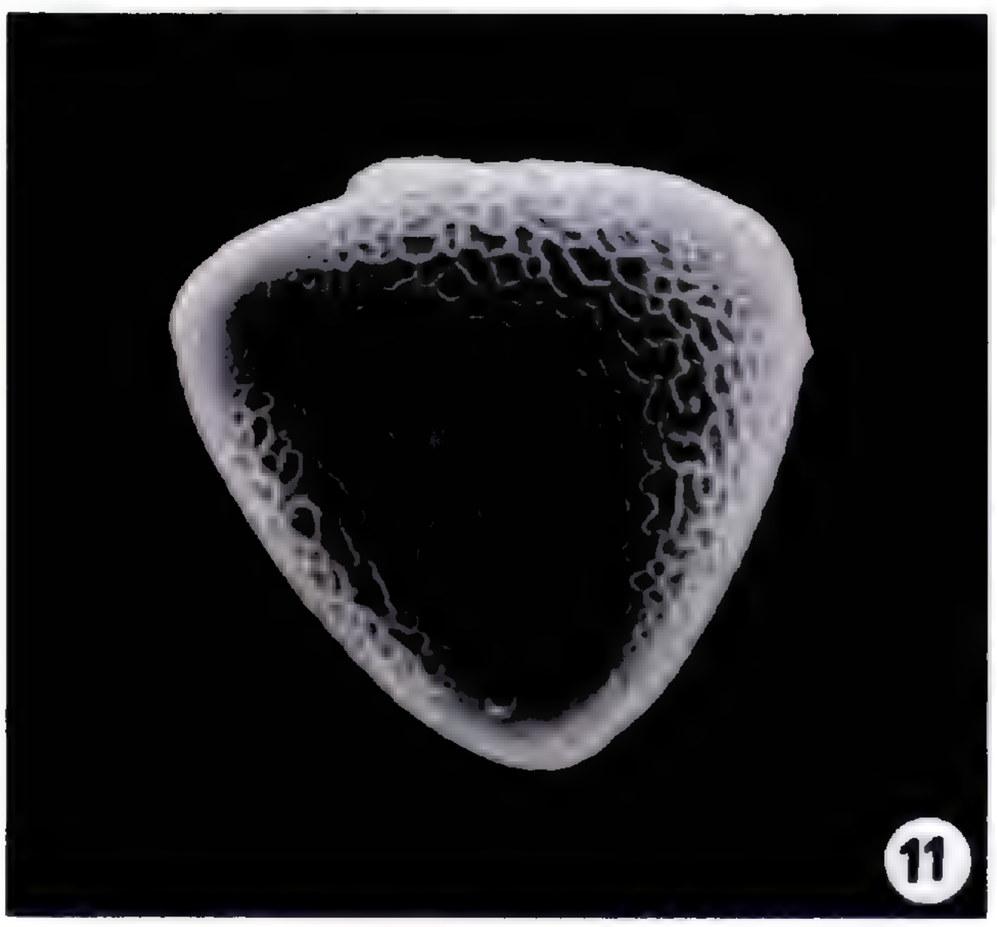
FIGURES 1–6. Whole pollen grains and exine surfaces of pollen grains from species pollinated by passerine birds. 1–3. Whole pollen grains, ×1,500; *E. fusca* showing variation in the pollen of the species.—1. Type (a) showing small lumina (*Millar 13818*).—2. Type (d) showing dense sexinous granules (*Haniff 348*).—3. Type (c) showing more or less large lumina with discontinuous muri (*Irwin 48782*). 4–6. Exine surfaces, ×3,600.—4. *E. stricta* showing pollen of Type (a) with sinuous lumina and segmented muri.—5. *E. arborescens* showing pollen of Type (a) with small, sinuous/round lumina.—6. *E. subumbrans* (*Merrill 1950*) showing pollen of Type (c) showing sinuous/round lumina and dense sexinous granules.

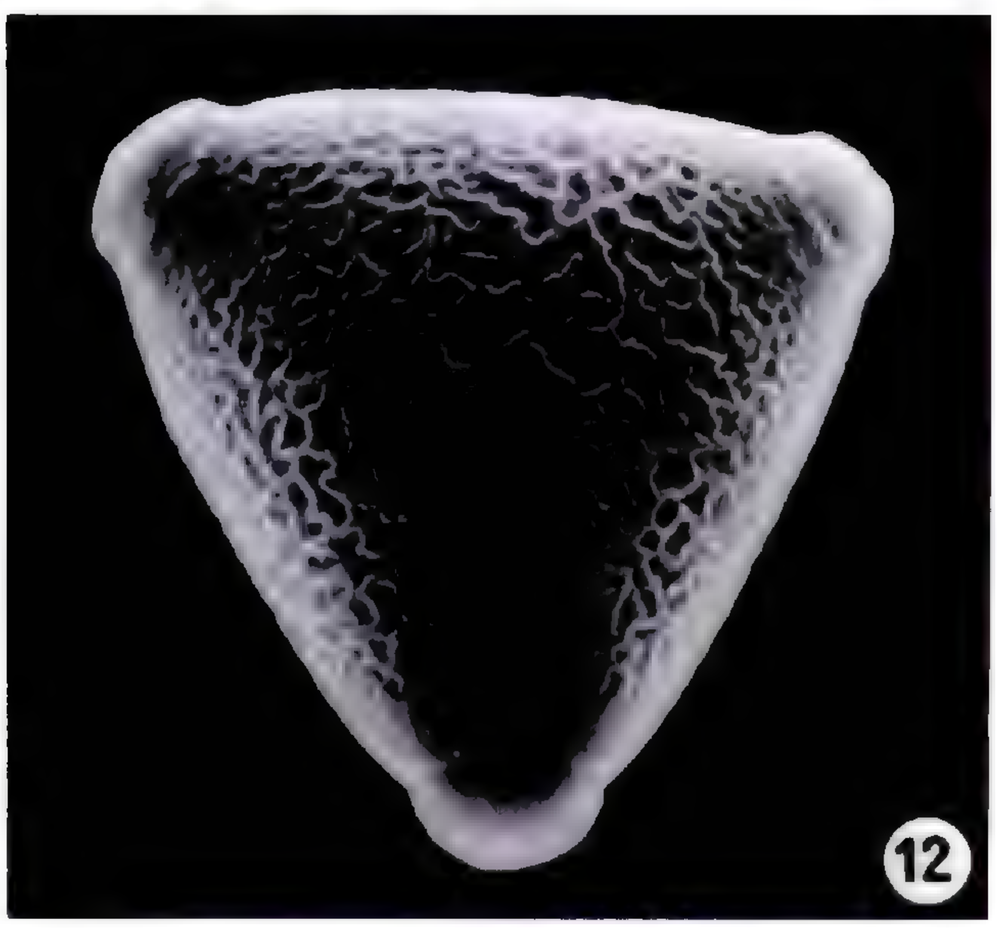




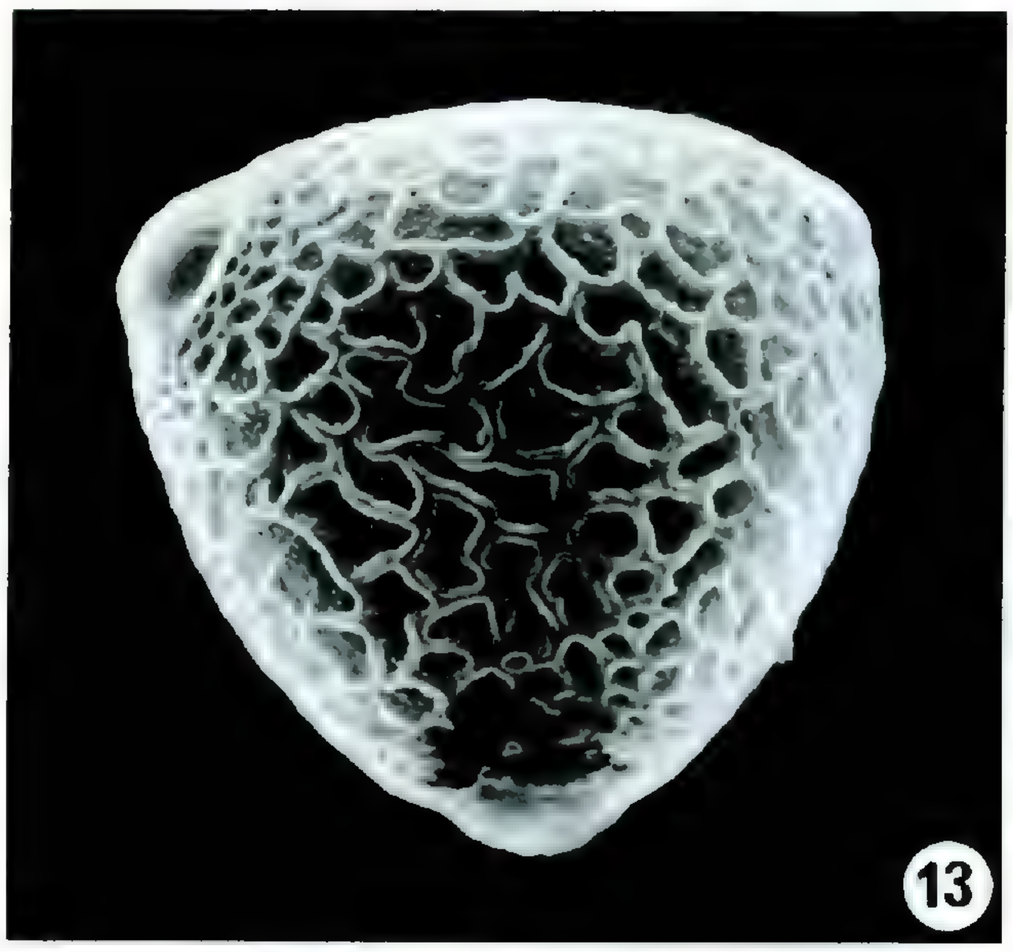


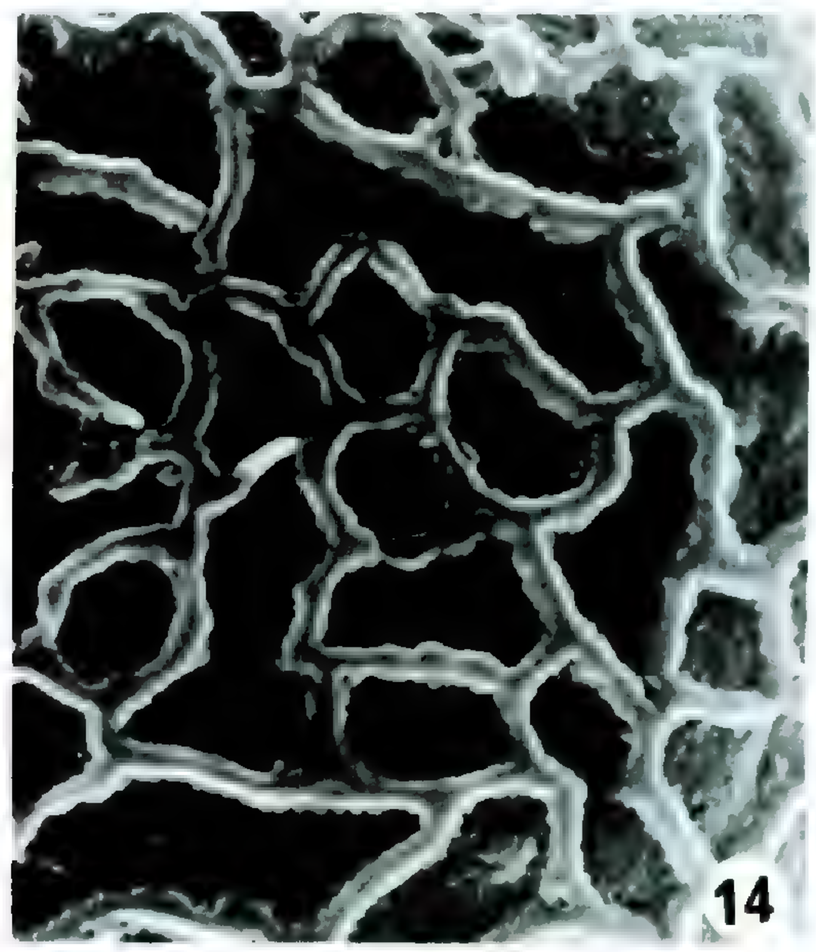


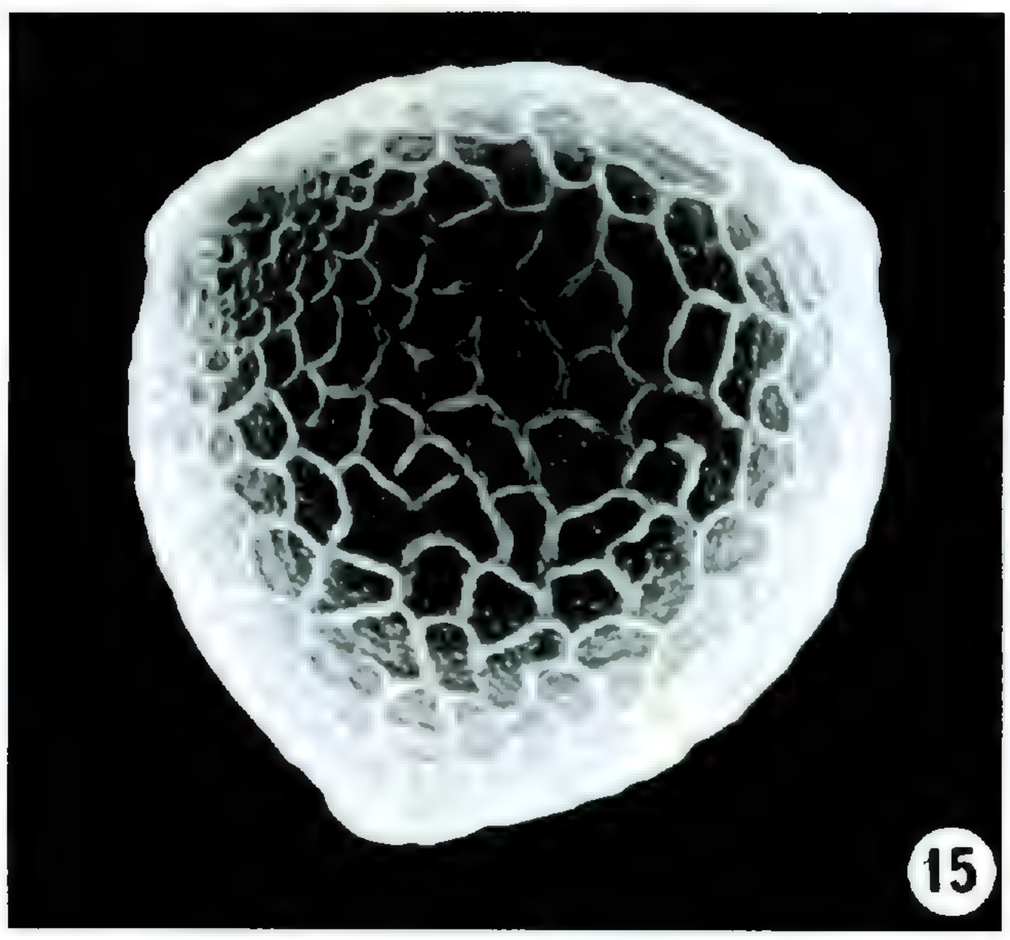


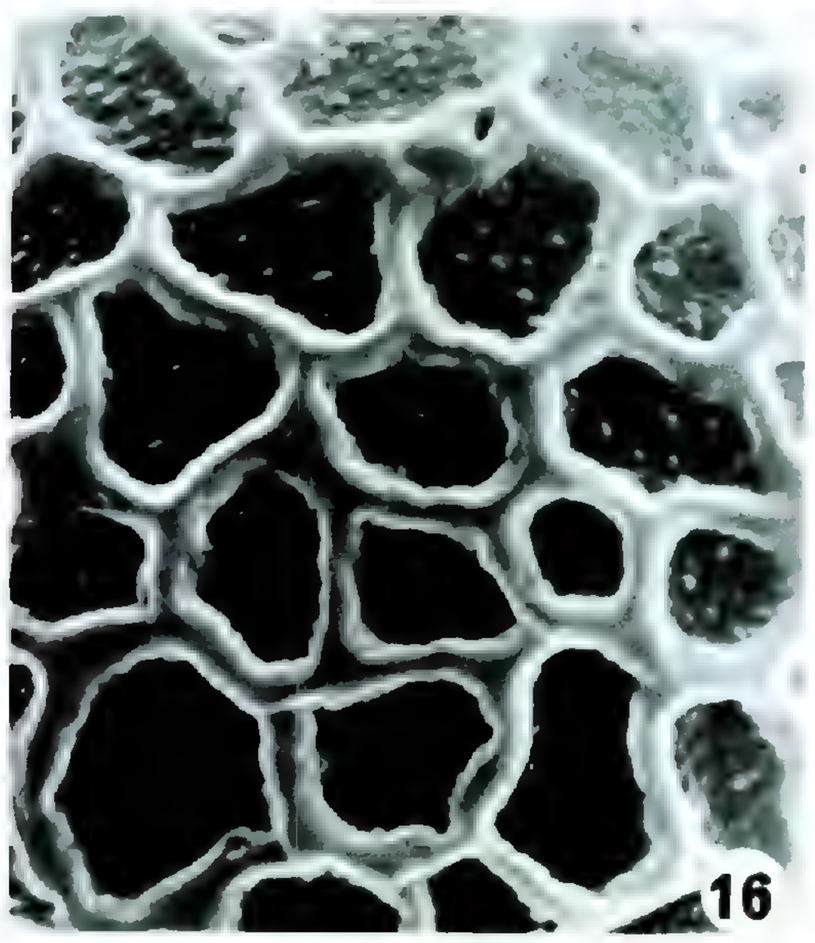


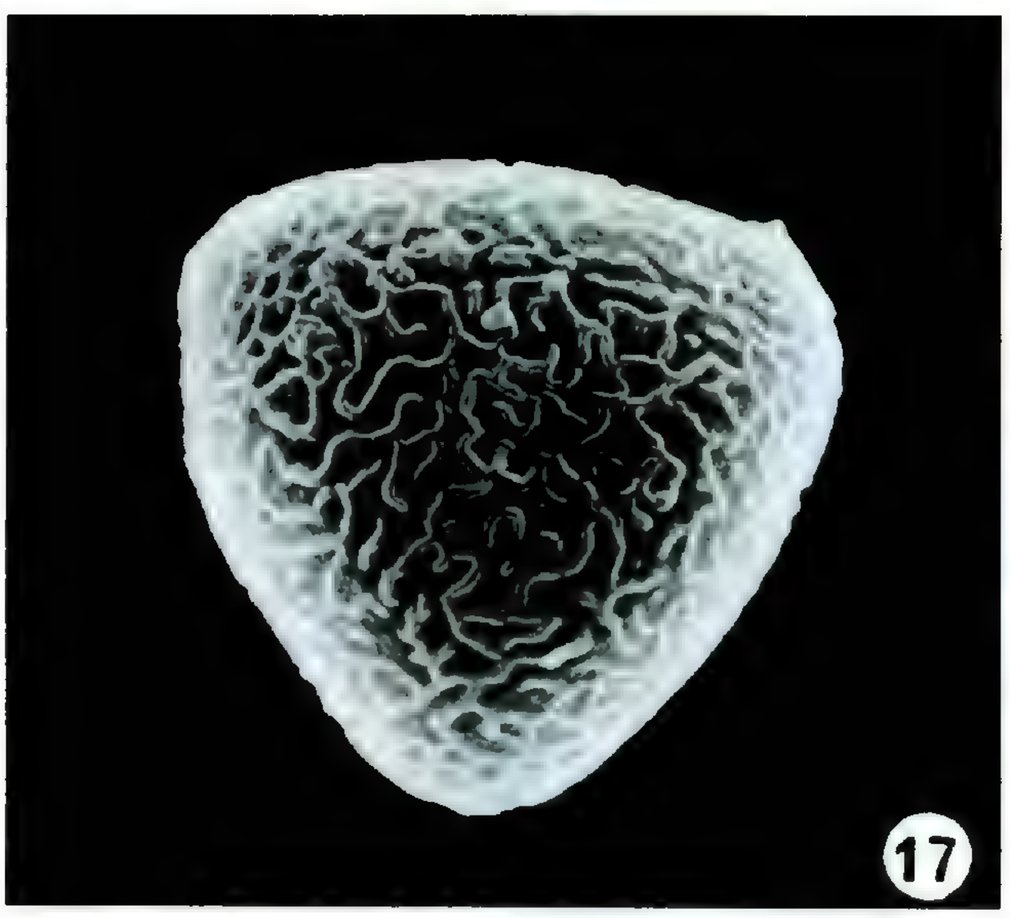
FIGURES 7–12. Whole pollen grains from species pollinated by passerine birds, ×1,500. All Type (a). 7–11. Showing small-sized pollen.—7. *E. crista-galli.*—8. *E. resupinata* (*Mooney 762*).—9. *E. arborescens.*—10. *E. breviflora* (*McVaugh 13210*).—11. *E. edulis.*—12. *E. oliviae,* medium-sized pollen.

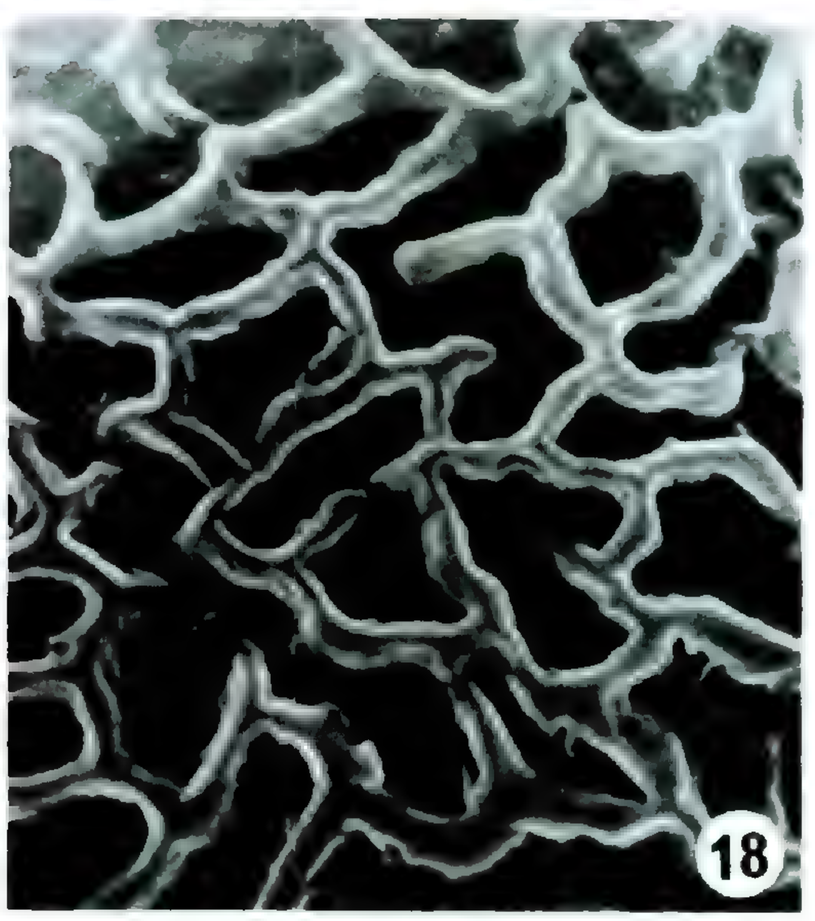




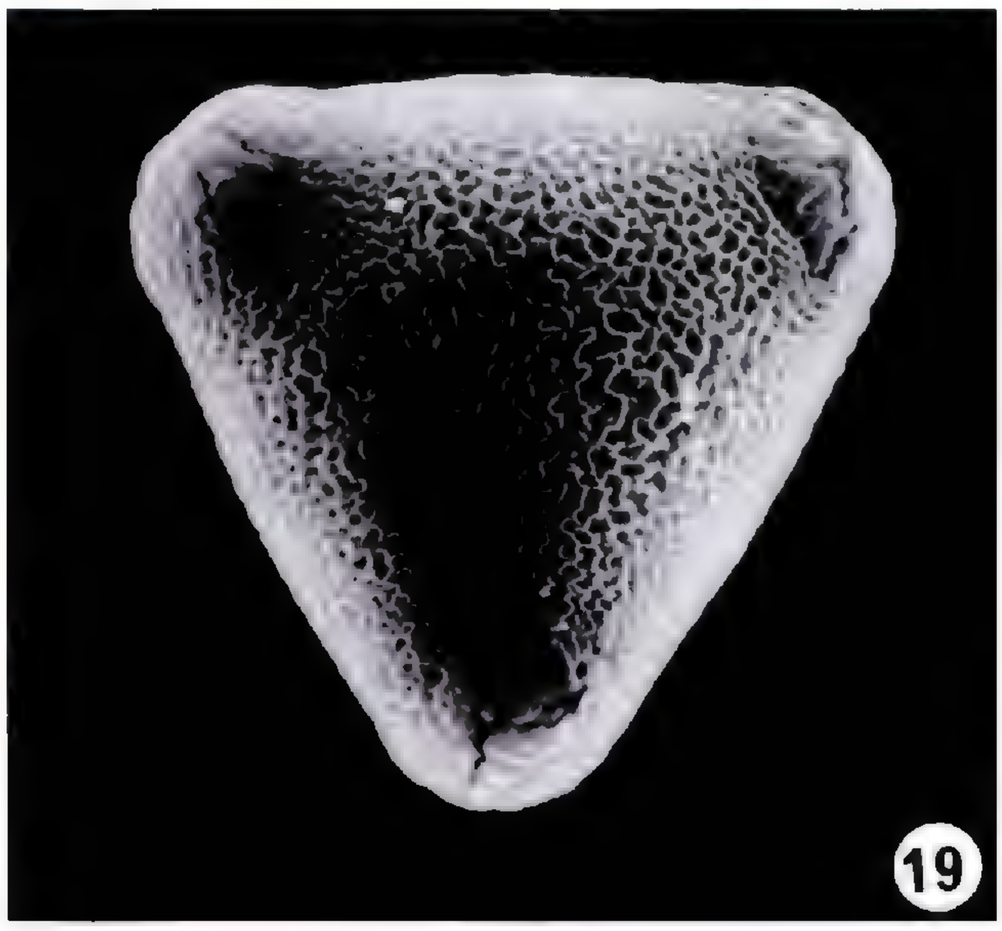


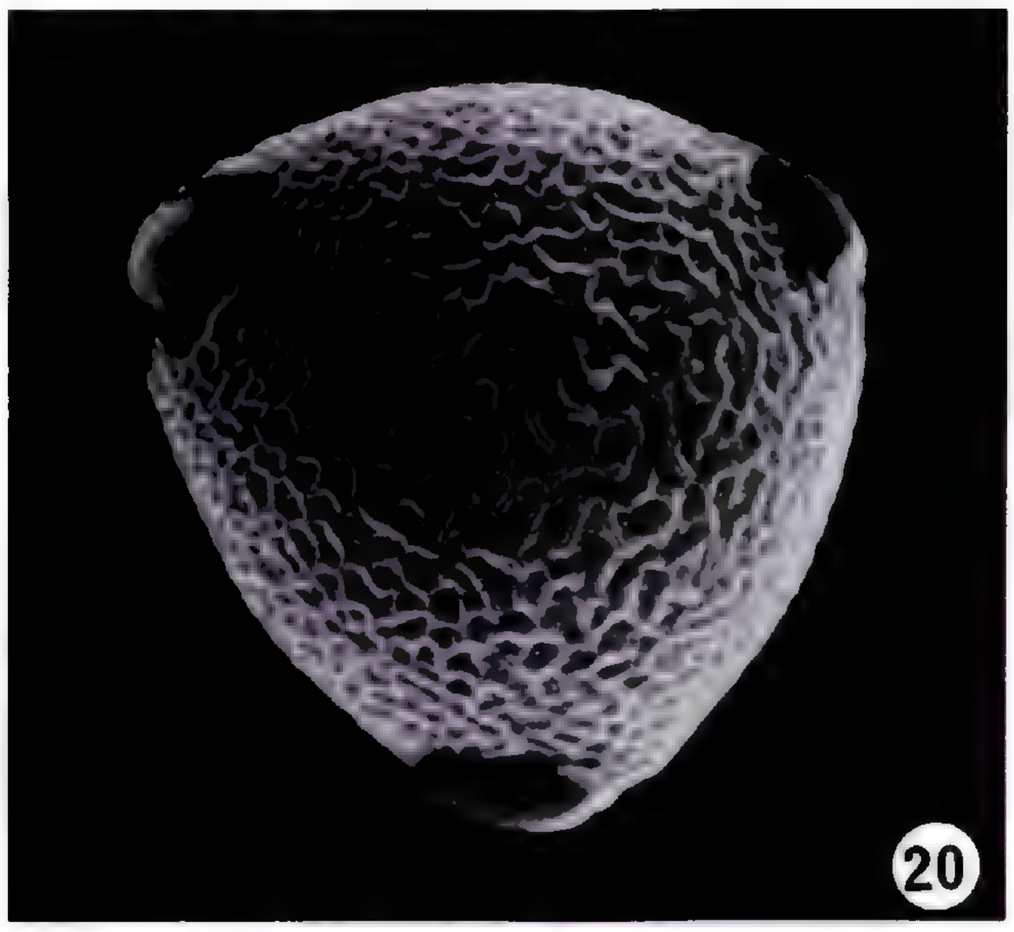


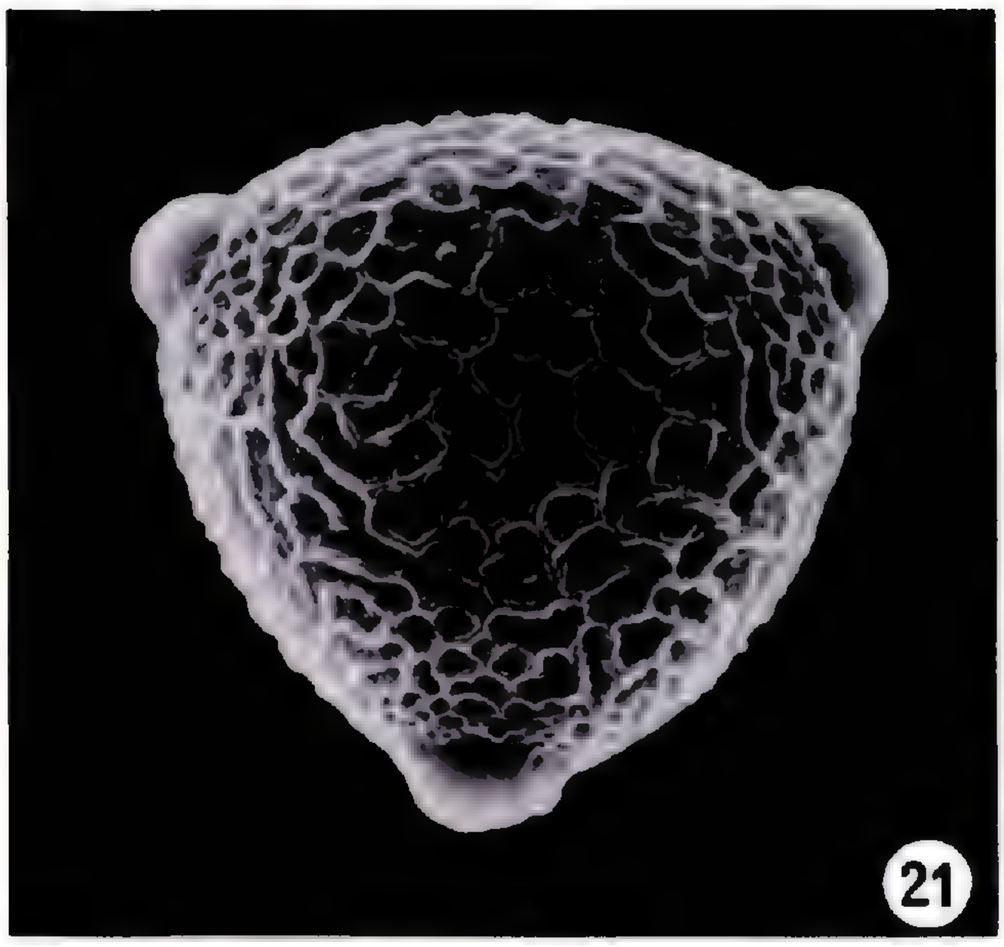


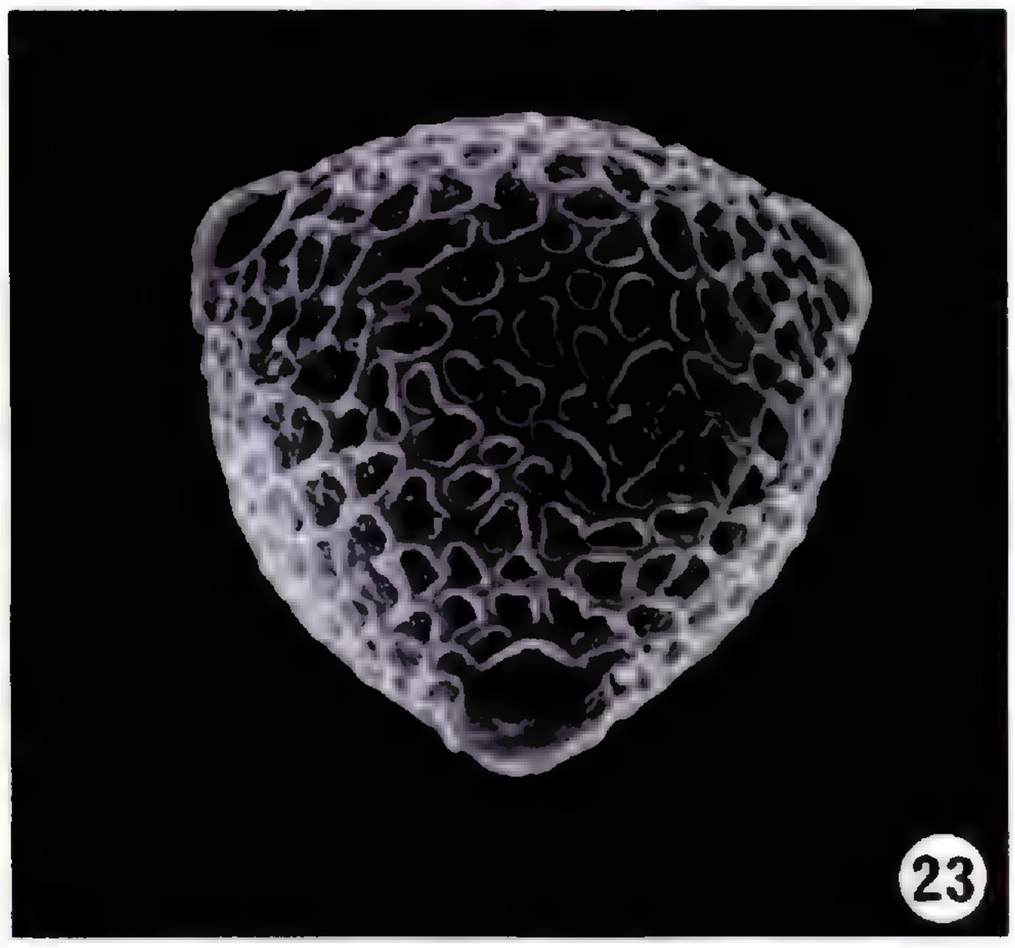


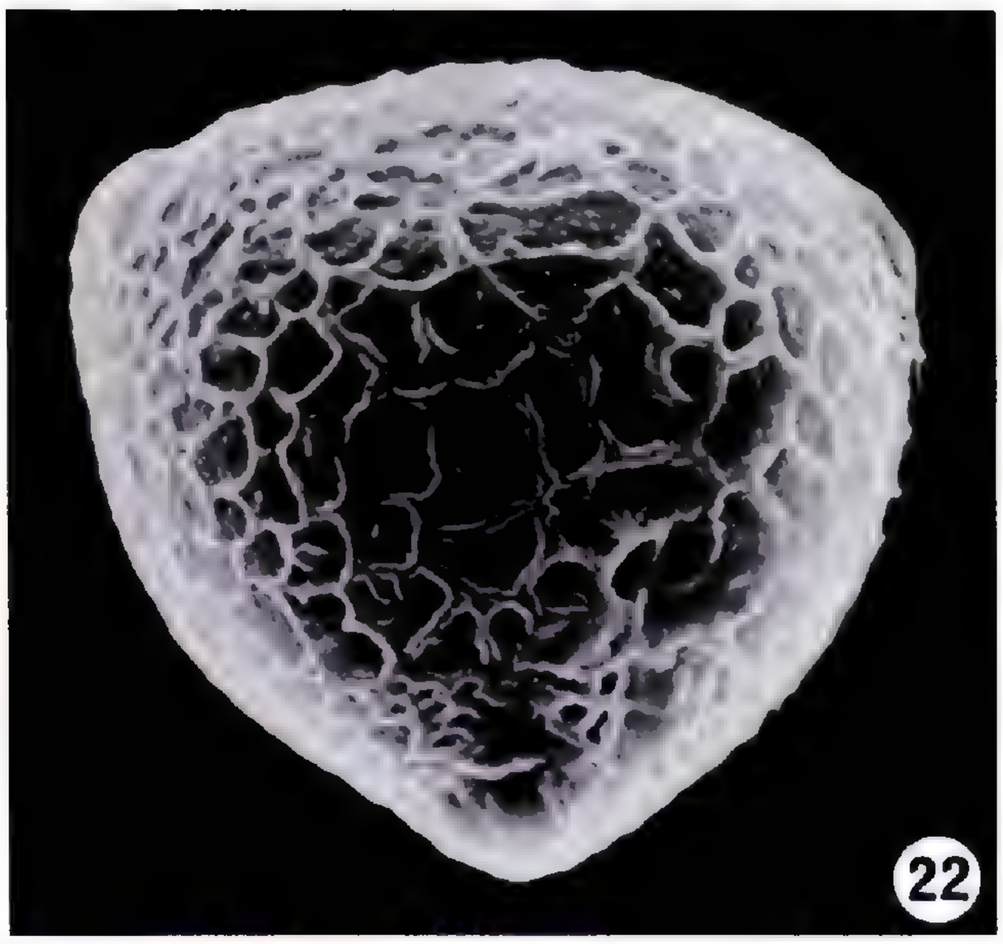
FIGURES 13–18. Whole pollen grains and exine surfaces of pollen grains from species pollinated by hummingbirds. All Type (b); 13, 15, 17, ×1,500; 14, 16, 18, ×3,600. 13, 14. Showing sinuous/round lumina, sexinous granules absent.—13. *E. barqueroana.*—14. *E. tajumulcensis.* 15, 16. Showing more or less round lumina with sparse very low sexinous granules.—15. *E. pudica.*—16. *E.* aff. *coralloides.* 17, 18. Showing sinuous lumina with muri sometimes discontinuous.—17. *E. leptopoda.*—18. *E. mexicana.*

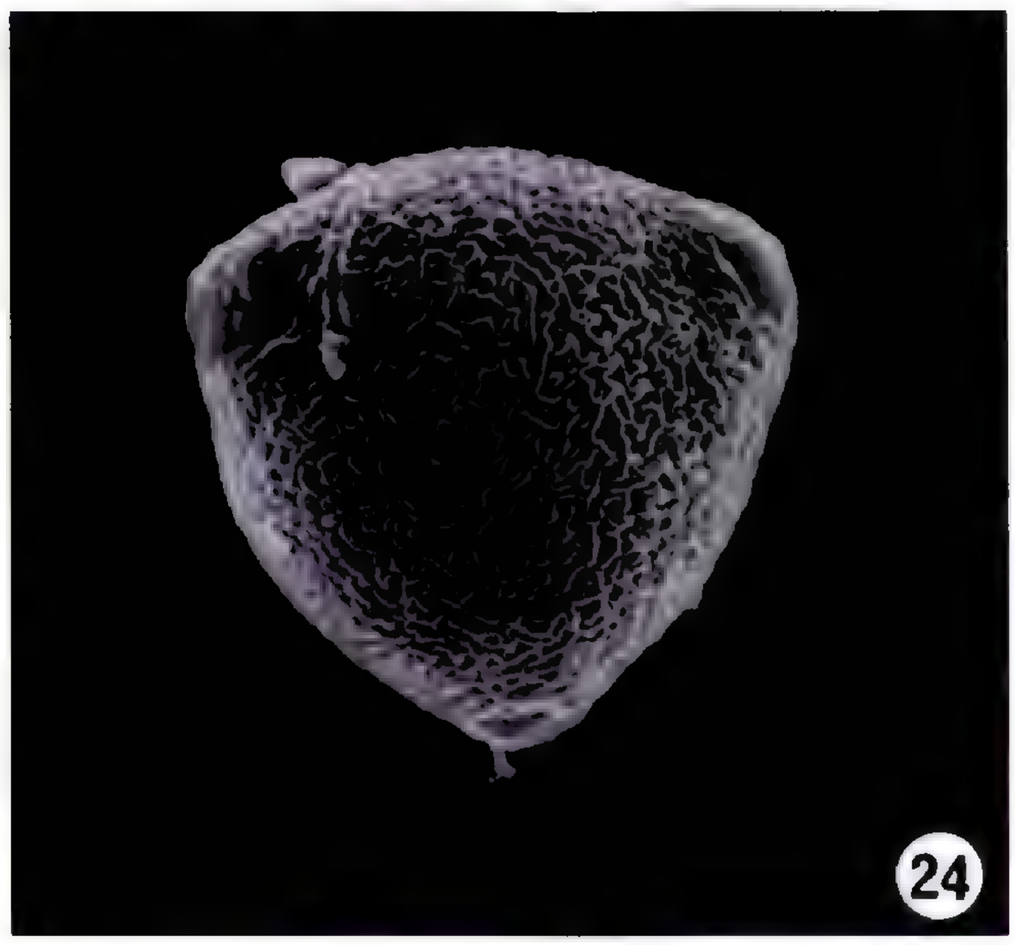




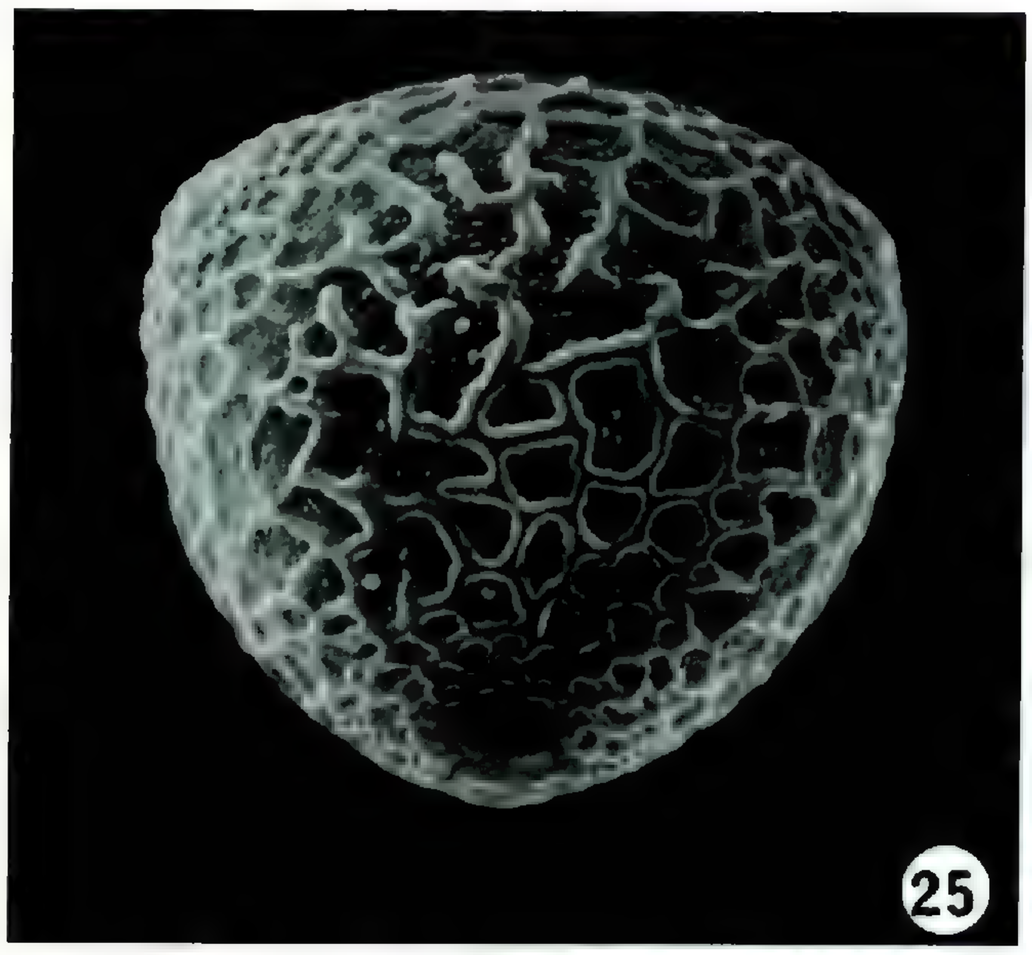


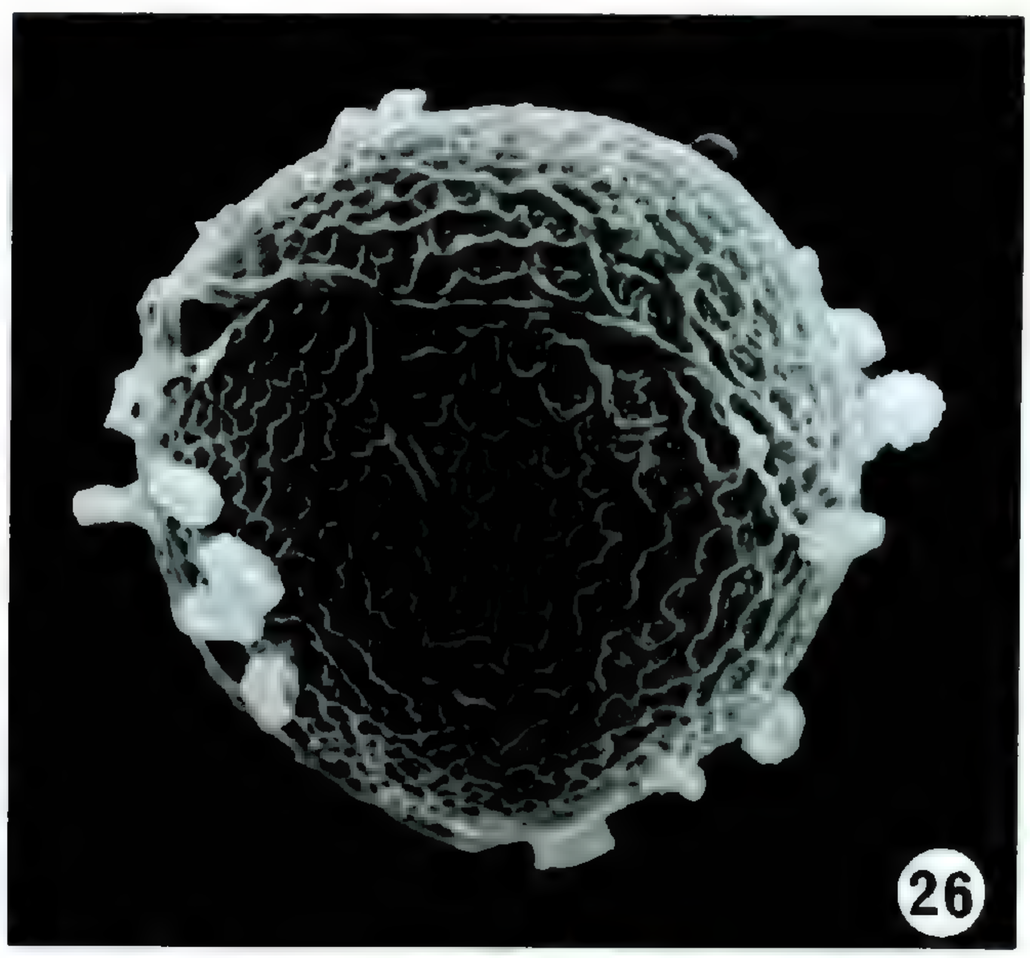


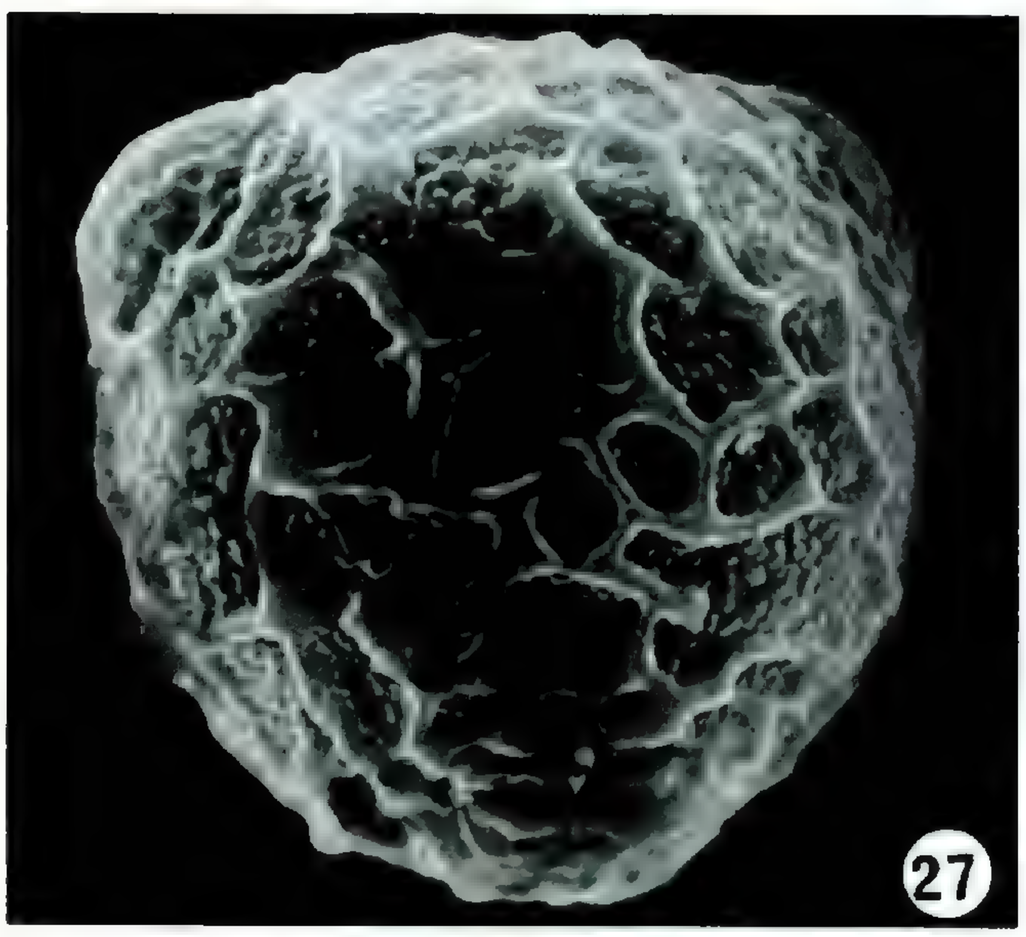


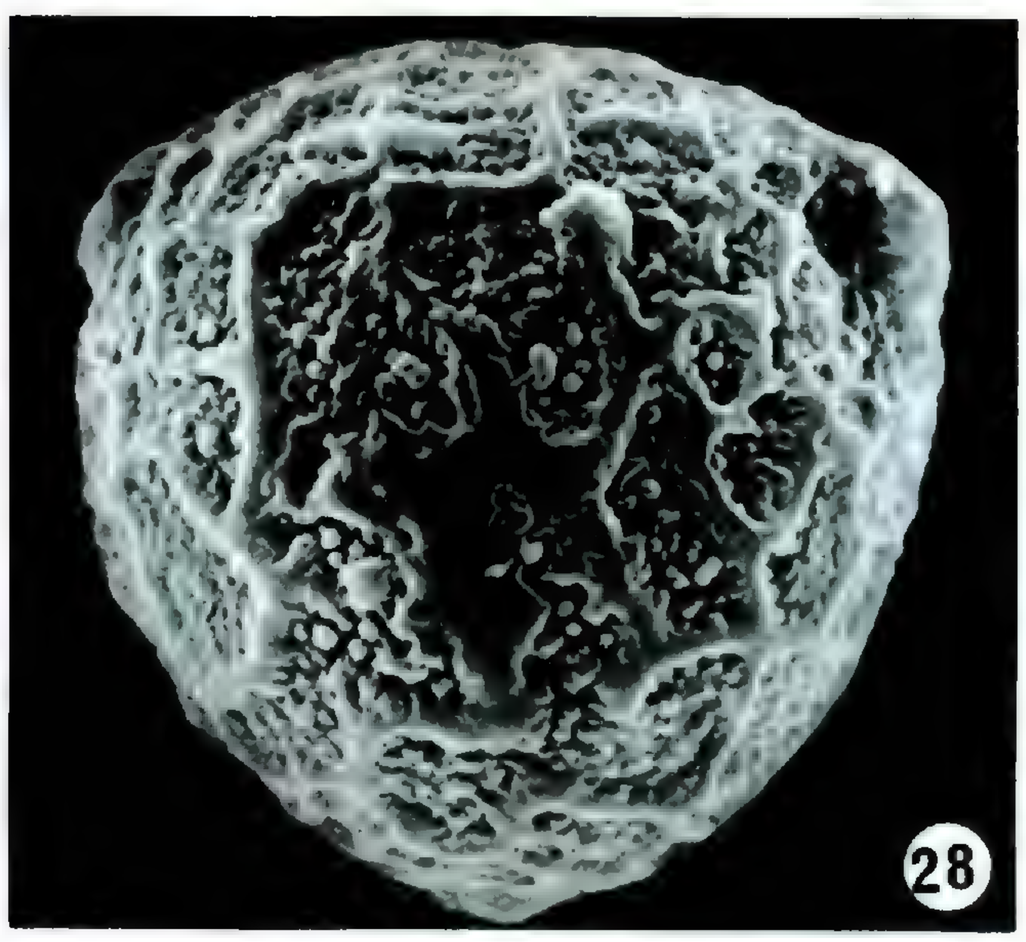


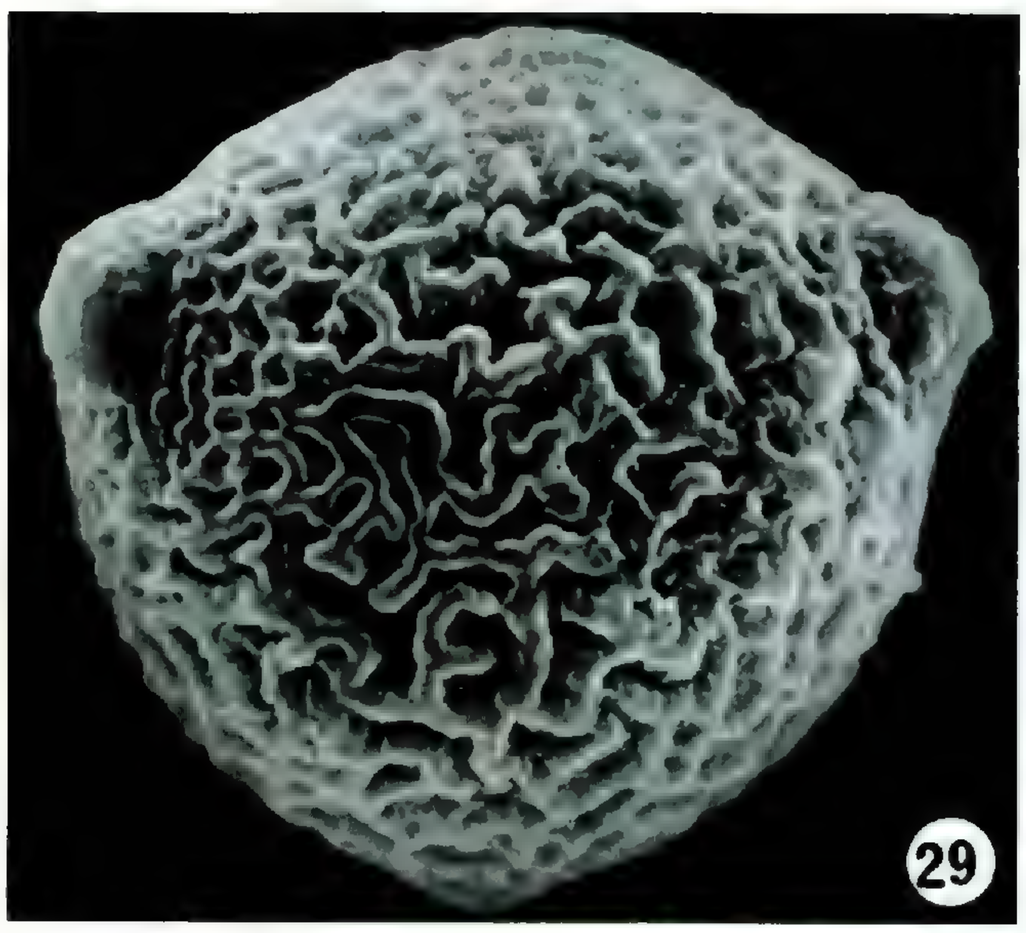
FIGURES 19–24. Whole pollen grains, ×1,500. 19–21. From species pollinated by hummingbirds that have atypical pollen in comparison with that of most other hummingbird-pollinated species.—19. *E. horrida* showing pollen of Type (a) with small lumina.—20. *E. speciosa* showing pollen intermediate between Types (a) and (b) with rather small, sinuous lumina and some low sexinous granules.—21. *E. pallida* (*Richards s.n.*) showing pollen of Type (c) with numerous sexinous granules. 22–24. From species pollinated by sunbirds.—22. *E. humeana* (*Codd 9297*) showing pollen of Type (b) similar to that found in most hummingbird-pollinated species (see Figs. 13–18). 23, 24. *E. zeyheri* showing variation in pollen of species.—23. Showing pollen with rather smaller lumina and broader muri than typical Type (b) and sexinous granules (*Holub s.n.*).—24. Showing pollen of Type (a) with small lumina (*Rogers 14814*).

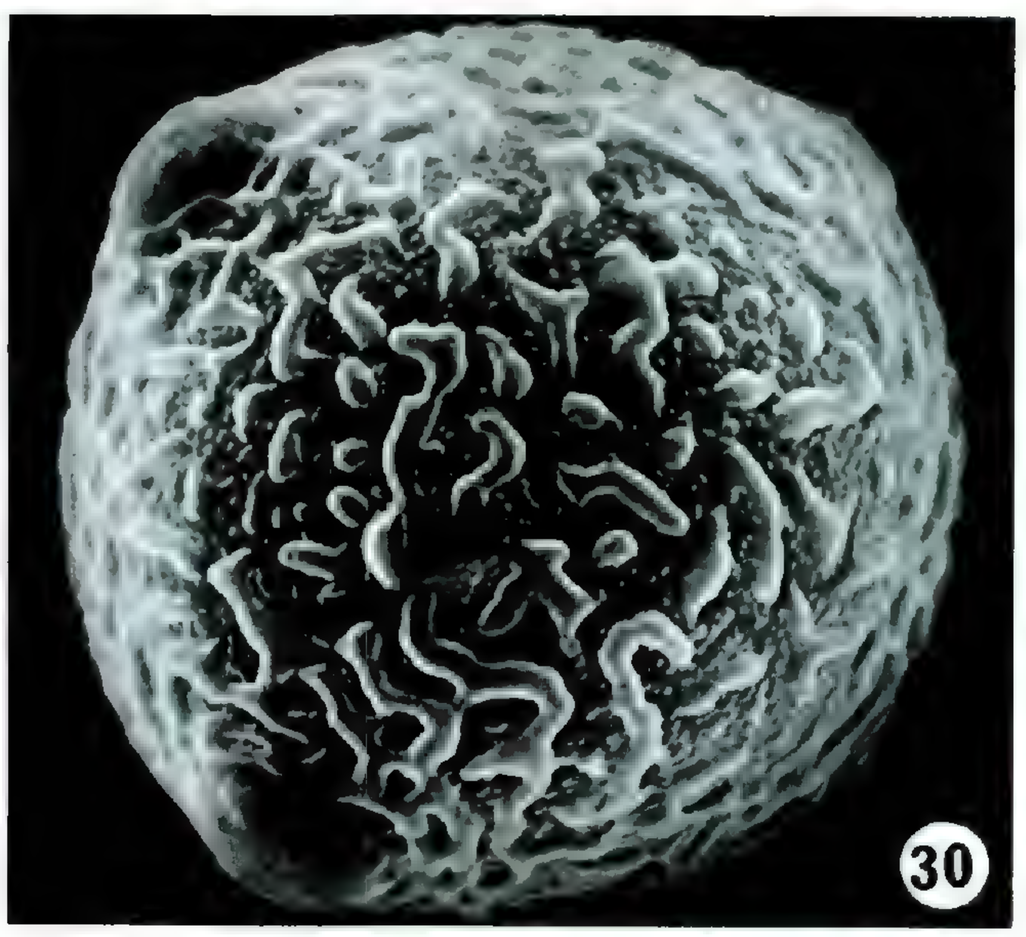












FIGURES 25–30. Whole pollen grains from species pollinated by passerine birds, ×1,500. 25, 26. Pollen of Type (c).—25. *E. mendesii* showing low sexinous granules and relatively broad muri.—26. *E. abyssinica* (*Hornby 926*) showing atypically small lumina and sexinous granules. 27–30. Pollen of Type (d) showing large-sized pollen with broad muri.—27. *E. latissima* showing large lumina and numerous sexinous granules.—28. *E. variegata* (*Rudd 3096*) showing very large granules.—29. *E. melanacantha* showing sinuous lumina and somewhat discontinuous muri.—30. *E. burtii* showing a 4-porate pollen grain with very discontinuous muri.

"hummingbird flowers" in subgenus *Erythrina*. Notable exceptions are *E. pallida, E. corallodendron, E. speciosa,* and a second sample of *E. coralloides* (*Krukoff 1970-124*), which have moderate granularity. Outside these "hummingbird"-pollinated sections, granules are absent or low on the pollen of a number of passerine-pollinated species, although their absence is frequently associated with smaller than average lumina size (e.g., see Figs. 7–12) or broad muri (e.g., see Fig. 29). However, species in sections *Cubenses, Caffrae,* and *Humeanae* (subgenus *Erythrina*), and *E. haerdii* and *E. livingstoniana* in subgenus *Chirocalyx,* have absent or low granules and medium lumina size and muri width. All remaining species have moderate granularity.

EXINE STRATIFICATION

Thin sections for transmission electron microscopy of acetolysed exines were cut off a number of representatives from the range of variation found in the pollen to see if there were also differences in the exine stratification. No significant differences that were not already visible in SEM studies were apparent. Some details of the exine stratification are described in Larson (1964) and Ferguson and Skvarla (1981) and further information will be illustrated elsewhere.

INTRASPECIFIC VARIATION

If comparisons of pollen types between species are to be valid, it is important to have some idea of the degree of variability within species. From the above results, this is evidently considerable in certain species. Of the repeat samples examined, *E. poeppigiana, E. coralloides, E. pallida, E. humeana, E. abyssinica,* and four of the five specimens of *E. variegata* from different geographical regions were found to be consistent. *Erythrina variegata* from New Guinea, with its lack of reticulation and small size, appears to be anomalous.

One sample of *E. resupinata* showed incomplete development of the reticulum with granules on the polar faces; and one sample of *E. lysistemon* had unusually low relief of muri and lack of granules, not unlike the ornamentation on the pollen from an anther of deformed pollen of *E. goldmanii.* Perhaps these features are abnormalities of development. One sample of *E. zeyheri* had a much finer reticulum than another, and one sample of *E. burana* had broader lumina with flatter muri than the other.

The most variable species found was *E. fusca,* which had both broad and fine reticula, large and small size, and one without any apparent organized reticulum. All seemed to show evidence of moderate to high granularity.

POLLEN TYPES

The pollen of *Erythrina* can be divided into four main types described below. The pollen type to which each species is assigned is shown in Table 1. Two additional types (e) and (f) have been established for convenience.

Type (a). Pollen usually small in size (rarely medium or large), often markedly triangular in shape, with small or very small lumina, usually without visible sexinous granules (Figs. 1, 4, 5, 7–12, 19, 24).

This type is found largely in species pollinated by passerine birds with the exception of *E. horrida.* The species included are mainly in subgenus *Erythrina* sections *Suberosae, Arborescentes, Breviflorae,* and *Edules. Erythrina speciosa* and *E. schimpfii* are intermediate between Type (a) and Type (b).

Type (b). Pollen medium-sized (rarely large), rounded-triangular in shape, with medium-sized lumina, muri of medium width, very sparse or no sexinous granules present (Figs. 13–18, 22, 23).

This occurs in the New World species pollinated by hummingbirds that comprise sections *Leptorhizae, Erythrina, Gibbosae,* and *Corallodendron* together with S. African *E. humeana* and *E. zeyheri,* which are pollinated by sunbirds. *Erythrina poeppigiana* (section *Micropteryx*) and *E. haerdii* (section *Chirocalyx*) are pollinated by passerine birds.

Type (c). Pollen medium, sometimes large, in size, with medium-sized lumina, medium to broad muri, sexinous granules numerous and lower than height of muri.

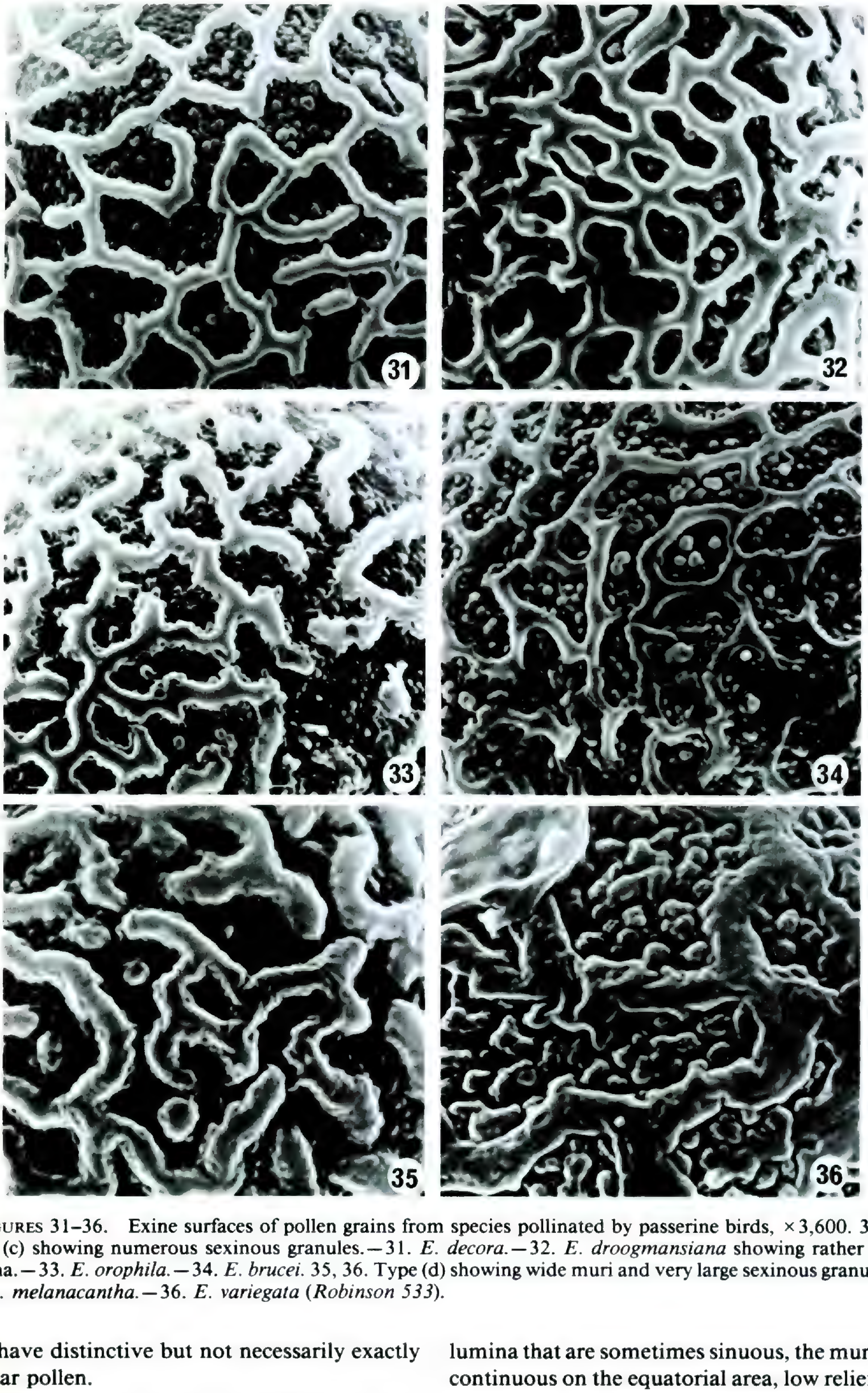
This type occurs primarily in subgenus *Chirocalyx,* among African species pollinated by passerine birds (Figs. 3, 6, 21, 25, 26, 31–34).

Type (d). Pollen large, lumina variable in size, muri broad, usually large, dense sexinous granules present (Figs. 2, 27–30, 35, 36).

This occurs in Old World species of subgenus *Erythraster* pollinated by passerine birds.

Type (e). Pollen usually medium-sized with very discontinuous muri on equator or poles or on both, muri merging into sexinous granules.

This occurs in five or more unrelated species



FIGURES 31–36. Exine surfaces of pollen grains from species pollinated by passerine birds, ×3,600. 31–34. Type (c) showing numerous sexinous granules.—31. *E. decora*.—32. *E. droogmansiana* showing rather small lumina.—33. *E. orophila*.—34. *E. brucei*. 35, 36. Type (d) showing wide muri and very large sexinous granules.—35. *E. melanacantha*.—36. *E. variegata* (*Robinson 533*).

that have distinctive but not necessarily exactly similar pollen.

Type (f). Pollen usually medium-sized with small, round lumina on the polar area and wide lumina that are sometimes sinuous, the muri discontinuous on the equatorial area, low relief sexinous granules present.

This occurs only in *E. merrilliana* and *E. tahi-*

tensis (subgenus *Erythraster*) that occur in the Pacific.

OCCURRENCE OF POLLENKITT

During the course of dissection of the flowers to remove pollen, it was noticed that pollen from the tubular, "hummingbird flowers" was consistently dust-like and easily spread, while pollen from other, gaping flowers often had a tendency to be more sticky and difficult to separate. In order to see whether this might have any basis, whole anther preparations and groups of pollen grains of several species were examined under the electron microscope. Of the "hummingbird flower" anthers and pollen groups examined, and in some other species such as *E. humeana* and *E. lysistemon* (visited by sunbirds), only very slight quantities of amorphous material or none at all could be seen between the pollen grains. Although of uncertain chemical identity, this substance may be described by the general term "pollenkitt." Variable quantities of pollenkitt were present, from little or none to quite large amounts, in groups with "passerine flowers." *Erythrina fusca, E. euodiphylla, E. velutina,* and *E. variegata* were all found to have moderate to high quantities, while species such as *E. mendesii, E. dominguezii, E. verna,* and *E. resupinata* showed variable or irregular occurrence of pollenkitt. Ferguson (1984) illustrated these differences in the occurrence of pollenkitt in *Erythrina* and briefly discussed the phenomenon in some other papilionoid legumes.

Changes occur in the composition and nature of the lipidic substances on the pollen wall prior to and at dehiscence of the anther (Hesse, 1981 and pers. comm.). These changes may occur to different degrees as a result of the methods used in the preparation of herbarium specimens. In view of this the differences found in stickiness may not be a true representation of the pollen under natural conditions. Investigations of fresh material would be interesting.

DISCUSSION

The reticulate ornamentation of the exine of *Erythrina* pollen evidently shows considerable morphological variation between, and sometimes within, species. How far may such variation be explained in terms of an adaptive response to the pollen vector?

In order to tackle such a question, a number of aspects of the pollination biology of the genus must be considered. Especially in such a large and complex pantropical genus such as *Erythrina,* our knowledge of the detailed pollination biology of each species is necessarily incomplete. Nonetheless, a few generalizations may be made. All species of *Erythrina* are pollinated primarily by birds that do not appear to discriminate between species (Raven, 1974); any one plant is likely to be visited, and pollinated, by a wide variety of local bird species (e.g., see Feinsinger et al., 1979; Guillarmod et al., 1979; Hernandez & Toledo, 1979; Morton, 1979; Raven, 1979; Steiner, 1979; Toledo & Hernandez, 1979). However, in the New World two distinct pollination syndromes exist, the tubular "hummingbird flowers" in six adjacent sections of subgenus *Erythrina* (*Stenotropis, Pseudoedules, Leptorhizae, Erythrina, Gibbosae,* and *Corallodendra*) and the more or less gaping flowers, pollinated predominantly by passerines (Raven, 1974). In the Old World, and therefore outside the range of hummingbirds, pollination is effected by a variety of passerine species in diverse families (Arroyo, 1981).

A number of other features of floral biology further distinguishes these two syndromes. Thus, in "hummingbird flowers" the inflorescence axis is vertical, with the individual flowers directed outwards, horizontally or somewhat deflexed, providing easy access to the nectar for a long-billed, hovering bird (Fig. 37A, B). By contrast, a typical passerine-pollinated species has a horizontal inflorescence axis, and the gaping flowers are directed inwards (Fig. 37E, F), permitting a bird perched on the horizontal axis to reach the nectar (Cruden & Toledo, 1977). Quantitative and qualitative differences between the nectars of passerine- and hummingbird-pollinated flowers have also been found. The former tend to produce more copious supplies of hexose-rich nectar, which also contains higher concentrations of amino acids, while the latter produce generally smaller quantities of nectar with a higher sucrose : hexose ratio (Baker & Baker, 1982).

A broad division of pollen types may also be made between these main pollination classes. Thus, "hummingbird type" pollen may be defined generally as medium-sized, with medium-sized lumina in the reticulum and none to sparse low sexinous granules [Type (b), Figs. 13–18]. By contrast, the pollen of passerine sections, in both the Old and New Worlds, is more heterogeneous in character with respect to both size and ornamentation. However, it may be distinguished

FIGURE 37. A, B. *E. chiapasana,* a typically hummingbird-pollinated species.—A. Showing a vertical inflorescence with flowers horizontal, pointing outwards, ×⅔.—B. Tubular flower, ×1. C, D. *E. falcata,* a passerine-bird-pollinated species with floral characters rather intermediate between those of the typical hummingbird and typical passerine bird type.—C. Showing a pendulous inflorescence with flowers more or less pointing outwards, ×⅔.—D. Showing a somewhat shorter tubular flower, ×1. E, F. *E. variegata,* a typical passerine-bird-pollinated species.—E. Showing a horizontally orientated inflorescence with flowers pointing inwards, ×⅔.—F. Showing a gaping flower with a broad reflexed standard, ×1.

generally from the "hummingbird type" either by moderate to dense granularity, or by markedly small lumina size. Some exceptions occur in both groups as discussed later.

The relative uniformity of pollen in the hummingbird-pollinated sections may indicate a relatively recent radiation of the group, and this is supported by Barneby (pers. comm.), who noted that these species are separated by much narrower morphological discontinuities than elsewhere in the genus. Conversely, the greater heterogeneity observed in passerine-pollinated sections may reflect the greater spread of taxonomic relationships consequent on a longer period of overall evolutionary divergence. But perhaps some adaptive advantage also underlies the observed differences between hummingbird and passerine pollen types, related to structural differences in the surfaces on which the pollen is carried. Neill (pers. comm.) indicated that the feathers of hummingbirds (and African sunbirds) may be finer at a microscopic level than those of larger passerine birds. Greenwalt (1960) stated that the hummingbirds may well be more closely feathered than any other bird family. The most striking feature of the plumage of hummingbirds is the iridescent patch of scaly "gorget" feathers found on the throat of the male and, in some species, extending over the head. These feathers have a quite different structure from the typical contour feathers of birds (Greenwalt, 1960). Furthermore, according to the observations of Neill (pers. comm.), the pollen of hummingbird-pollinated species is generally placed on the bill or very fine throat feathers of the bird, whereas that of passerine-pollinated species is placed on the coarser chest feathers of the bird (see also Cruden & Toledo, 1977; Toledo, 1974; Toledo & Hernandez, 1979).

As previously indicated, some overlap of pollen types does occur between the species of these two main pollination classes, but this is perhaps to be expected in a closely knit genus that is apparently still in a state of evolutionary flux with respect to pollination syndromes, and in which pollen morphology varies along a number of continua. For instance, pollen rather similar to the "hummingbird type" is found in a few Old World species. The southern African small section *Humeanae* in subgenus *Erythrina* is distinctive in having deflexed, tubular rather than gaping corolla and is apparently adapted for pollination by sunbirds (Cruden & Toledo, 1977; Guillarmod et al., 1979). The African sunbirds, though quite unrelated, show certain parallels with the New World hummingbirds in their degree of specialization as flower visitors (Stiles, 1981) and in the possession of patches of iridescent plumage, for example. However, the pollen of *E. zeyheri* in this section was found to show some variability (Figs. 23, 24). The neighboring small section *Caffrae,* found in the same region, has the more typical gaping flowers, and although sunbirds are frequent visitors to the flowers of *E. caffra* so are larger, less specialized passerines. Again, the pollen of *E. lysistemon* in this section was somewhat variable. Two other Old World species, *E. haerdii* and *E. livingstoniana* in subgenus *Chirocalyx,* have pollen not dissimilar to the "hummingbird type."

Visits from both hummingbirds and passerines are reported for several of the New World species in subgenus *Micropteryx* with more or less gaping flowers, including *E. poeppigiana* and *E. crista-galli* (Toledo, 1974). In the latter, the flowers are outwardly directed by virtue of their almost resupinate position, and it has been suggested that the resupinate position may be viewed as an alternative strategy to a straightened keel, allowing hummingbirds easy access to the nectar; the low sucrose:hexose ratio of the nectar, however, is consistent with perching bird pollination (Baker & Baker, 1982). The racemes of *E. dominguezii* and *E. falcata* are pendulous rather than horizontal, and the flowers less widely gaping than the typical passerine type, with the keel petal forming a short tube around the base of the stamens (Fig. 37C, D; see also Lucas & Theobald, 1982). Of these species, the pollen of *E. poeppigiana* most closely approaches the "hummingbird type," although that of *E. falcata* is only a little more granular; *E. crista-galli* differs in the small size of the pollen and the narrow lumina. *Erythrina cubensis,* placed in a monotypic section in subgenus *Erythrina,* has more or less tubular flowers, and although pollination data were not available, there seems no reason why it should not be hummingbird pollinated.

Among the hummingbird-pollinated sections, *Leptorhizae* is somewhat anomalous in having small or very small lumina size (Fig. 19). Romeo's (1973) chemotaxonomic data suggest affinities of *E. leptorhiza* (section *Leptorhizae*) with species of sections *Breviflorae* and *Edules,* and this is supported by the pollen morphology (Graham & Tomb, 1977): pollen in these sections is characterized by small lumina size and distinctly triangular amb (also found in sections *Suberosae, Arborescentes,* and *Oliviae*). Section *Breviflorae* is unusual in its pollination biology, containing

both the passerine-pollinated *E. breviflora* and *E. batolobium,* which also has gaping flowers, but the inflorescence is vertical, and the flowers are pollinated by medium-sized hummingbirds (Hernandez & Toledo, 1982). The pollen of both species is in general rather similar and not of the "hummingbird type." Perhaps these sections represent a cluster of species around the "evolutionary borderline" between pollination syndromes (Hernandez & Toledo, 1982). The other exceptions to the "hummingbird type" pollen are *E. speciosa* (section *Stenotropis*) and *E. schimpffii* (section *Pseudoedules*) with smaller than average lumina size (Fig. 20), *E. pallida* (Fig. 21) and *E. corallodendron* showing moderate granularity, and *E. hondurensis* with discontinuous muri.

A further feature of the pollen morphology was the sometimes quite considerable intraspecific variation. The most variable species encountered during this study was *E. fusca* (Figs. 1–3), although other species also showed some variability. *Erythrina fusca* is the most widespread species in the genus, occurring on all four continents, and was also considered by Krukoff and Barneby (1974) to be the most primitive. Perhaps this variability in pollen morphology is an indication of the greater plasticity of expression of a relatively unspecialized genotype. Or perhaps it is a function of the wide distribution and long evolutionary history, permitting local differentiation of pollen types.

From the foregoing, it may be seen that although a broad correlation can be made between pollen morphology and pollen vector, this is subject to several constraints. However, as previously mentioned, many gaps still remain in our knowledge of the plant-pollinator relationships in the genus, and such relationships are not always straightforward. A thorough comparative study of the structural differences between the surfaces of the pollen vectors and the physical interactions with the pollen surface is a complex field, outside the scope of this investigation. In this context, it should be noted that the actual surface of interaction between pollen and pollen vector may well not be the exine itself but an adhering layer of tapetal-borne materials (pollenkitt). Hesse (1981) has suggested that the exine sculpturing may influence the distribution and adhesion of pollenkitt on the surface of the exine, thereby modifying the stickiness of the pollen. During this study, several of the passerine-pollinated species were found to have an abundance, or irregular and variable distribution of pollenkitt over groups of pollen grains, whereas this was not apparent in hummingbird flowers. Maybe the presence of sexinous granules facilitates the adherence of pollenkitt by providing a "key"; prominent granules or closely packed muri perhaps may support the layer of pollenkitt at the outermost surface of the pollen grain, where it is most effective.

Questions are raised as to the plasticity of exine sculpturing at an evolutionary, ecological, or developmental level. How strong a selective pressure must operate to disrupt established patterns of exine ornamentation influenced more by evolutionary relationships than present pollination ecology? How long must the relationship between plant and pollen vector have been established before any modification of the pollen surface becomes apparent? What is the effect of the simultaneous activity of numerous pollinators on possibly quite different surface structures? Can adaptation of pollen ornamentation occur at a populational level in response to locally operating pollinators? How far, and in what way, do other roles of the pollen surface, for example, interactions with the stigma (Heslop-Harrison, 1979), influence the form of the exine sculpture? How sensitive is the form of the reticulum to minor fluctuations in, for example, temperature or humidity (Hebda & Lott, 1973) during development? Any or all of such factors, or many others, may interact to determine the nature and extent of the variation observed on the pollen surface.

Conclusions

Although considerable variation occurs in the exine ornamentation of the pollen of *Erythrina,* some general conclusions can be drawn from this study. New World species of *Erythrina* with long, slender, horizontally presented, tubular flowers and vertical inflorescences adapted to pollination by hummingbirds tend to have similar medium-sized pollen with a simple, regular, reticulate ornamentation and no sexinous granules in the lumina. Species with more or less gaping flowers held reflexed with the standard petal enlarged, with horizontal inflorescences that occur in both the Old and New World, and that are pollinated by passerine birds have pollen grains that are much more varied in size and ornamentation with almost always either small lumina or sexinous granules present. The variation in the pollen morphology of passerine-bird-pollinated species may reflect the large range of types of

birds involved as much as taxonomic and morphological differences.

Pollen from hummingbird-pollinated species appears to be dry and powdery when dissected from anthers taken from herbarium specimens while that of many passerine-bird-pollinated species appears to be rather sticky.

The observations suggest some modification of pollen morphology in response to pollen vector.

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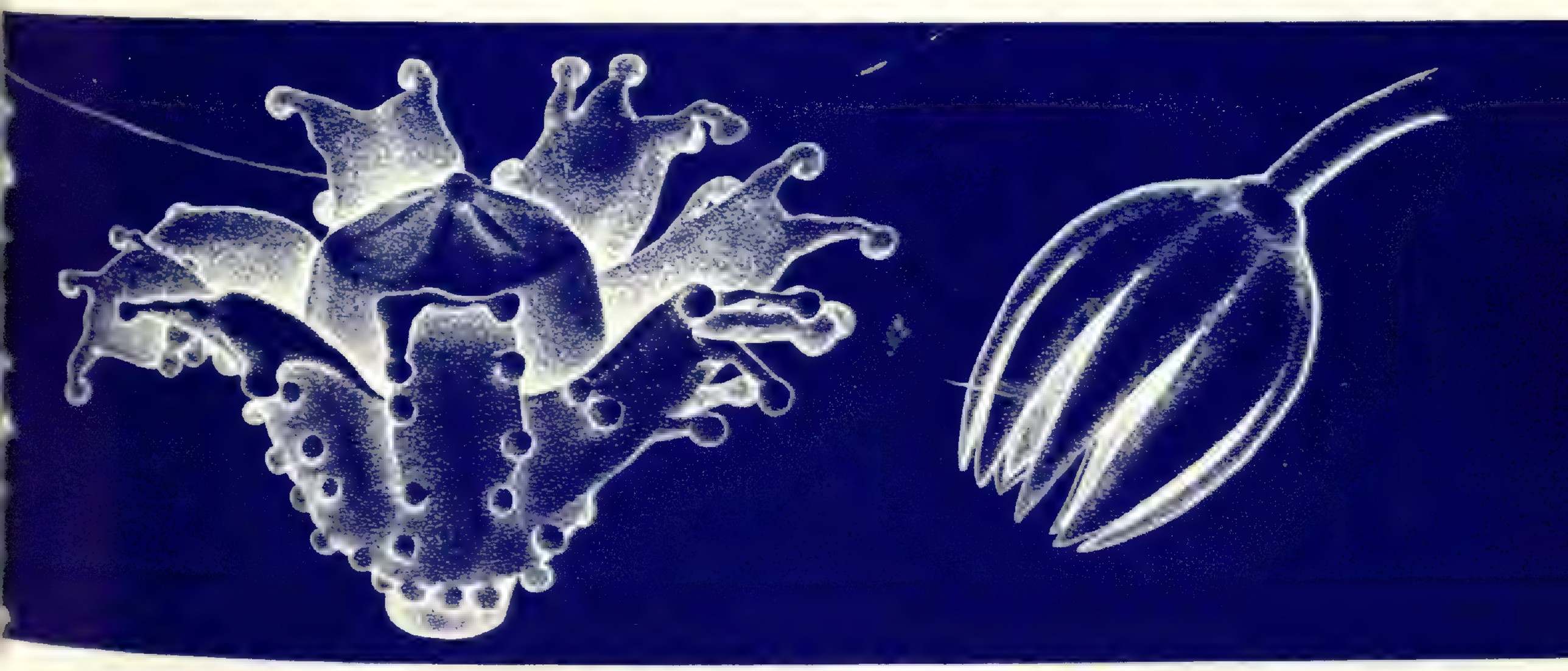

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THE IMPLICATIONS OF PHYLOGENETIC ANALYSIS FOR COMPARATIVE BIOLOGY: THE THIRTIETH ANNUAL SYSTEMATICS SYMPOSIUM

This symposium brings together seven systematic biologists to discuss the relationship between phylogenetic systematics (cladistics) and various branches of comparative biology. Cladistic theory and method were not the focus of this symposium, but rather it addressed how the results of cladistics—that is, hypotheses about phylogenetic pattern—are an essential component of historical analysis. Thus, the papers presented here illustrate six specific problems that, directly or indirectly, rely on cladistic analysis for their solution.

Cladistics became an important force within systematic biology following the English translation of Willi Hennig's "Grundzuge einer Theorie der phylogenetischen Systematik" (1950), which was updated in 1966 as "Phylogenetic Systematics." From that time, cladistics has steadily increased in influence, first within zoology, and somewhat later in botany (for an introduction to cladistics, see Eldredge & Cracraft, 1980; Wiley, 1980, 1981; Patterson, 1980; Nelson & Platnick, 1981; Cracraft, 1983; Humphries & Funk, 1984). During this period many workers have discussed the pros and cons of cladistics, and frequent misunderstandings about the theoretical and methodological content of cladistics have arisen. Perhaps contributing to this situation is the fact that the views of cladistic theoreticians have also evolved, often along divergent pathways so that the field of cladistics is now broader, and consequently more internally contentious, than it was 15 years ago. Despite this diversity, the question can be asked whether cladistics is united by any underlying principles so as to form a coherent research program. An answer to this question is of interest beyond being able to differentiate cladists or their work, because it also helps to place the various transformations of cladistics into a common framework and to gain a perspective on some of the arguments that are currently being expressed over the meaning and content of cladistic thought.

The Principles of Cladistics

We do not wish to engage in an extended discussion of the historical changes that have taken place in the thinking of individual cladists. We want, instead, to call attention to a common intellectual thread that has passed through the writings of cladists from Hennig to the present. We perceive this thread to consist of two principles: (1) taxa are united into natural groups on the basis of shared derived characters, or synapomorphies (the Principle of Synapomorphy), and (2) classifications must express those taxic patterns of synapomorphy explicitly (the Principle of Strict Monophyly). To be sure, each of these principles may rely on certain unexpressed assumptions, but none we think that are not also shared with noncladistic methods of systematics. For instance, Platnick's (1979: 538) first principle of cladistics, that nature has a single historical pattern with a hierarchical structure, would probably be acceptable to the majority of systematists.

With respect to these two principles, the Principle of Synapomorphy is clearly primary in that the Principle of Strict Monophyly depends on it.

Pheneticists and their followers reject the first principle, and therefore, logically also reject the Principle of Strict Monophyly. Some evolutionary (or eclectic) systematists might well accept the Principle of Synapomorphy but advocate paraphyletic taxa, thereby rejecting the Principle of Strict Monophyly; in fact, however, we believe that most evolutionary systematists, like pheneticists, reject both principles.

We also suggest that a third principle has been central to cladistic theory and methodology, namely, the Principle of Strict Parsimony. Although an acceptance of parsimony is basic to all scientific reasoning, cladists have certainly been much more concerned with elucidating the relationship of parsimony to systematics and applying parsimony analysis to their work than have advocates of phenetics or evolutionary systematics. Some of the critical literature discussing the application of parsimony to systematic hypotheses includes Kluge and Farris (1969); Gaffney (1979); Farris (1982, 1983), Sober (1983a, 1983b), and Maddison et al. (1984).

Within a cladistic framework taxa are grouped on the basis of shared character transformations. All such characters are termed synapomorphies. Some of these transformations will be unique, others may have arisen more than once within the group being studied and may be termed homoplasious. Obtaining a final interpretation of the pattern of the character transformation for any specific character depends on the tree topology (phylogenetic hypothesis) upon which all character transformations are optimized. Thus, we choose that tree by maximizing the congruence of character transformations across the *entire* data set. Logically, this also implies that homoplasies are minimized, thus resulting in the fewest *ad hoc* hypotheses required to explain those character distributions (Wiley, 1975; Farris 1982, 1983). Within this methodological framework, it is clear that homoplasies (parallelisms, convergences, reversals) are also synapomorphies: they represent derived character transformations defining two or more unrelated groups of taxa ("unique" synapomorphies define only a single group).

The Principle of Strict Parsimony has been a core methodological component of mainstream cladistics for nearly two decades. In recent years, a small number of workers, also claiming to practice cladistics, have advocated abandoning (or at least relaxing) this principle in favor of a method that constructs trees using only a subset of the original character data. This method, called compatibility or clique analysis, unites taxa by utilizing those characters that exhibit congruence and eliminating those showing homoplasy (Estabrook et al., 1976; Meacham, 1984). Compatibility methods have been strongly criticized from several standpoints (Farris & Kluge, 1979; Mickevich & Parenti, 1980; Churchill et al., 1984). We note here the primary philosophical objection: a given scientific hypothesis, including those within systematics, has veracity compared to competing hypotheses when it best explains all of the relevant data, thus it is unclear to what extent hypotheses can be objectively compared when we exclude from consideration data that might be incongruent with one or more of the alternatives.

THE CHANGING FACE OF CLADISTICS

Cladistics emerged as a solution to a long-standing problem within systematic biology: how do we come to have knowledge about the phylogenetic relationships of organisms? Most contemporary systematists employing cladistic methods still see this as the central focus of their research. For all these workers, branching diagrams (cladograms) are interpretable as phylogenetic hypotheses and represent evolutionary history. Within this framework, synapomorphies are taken to be evolutionary transformations or derivations from more primitive conditions.

The preceding describes a view of cladistics sometimes termed "phylogenetic" or "evolutionary" cladistics. To most of its practitioners, an evolutionary process underlies the rationale for the method. A claim for a specific evolutionary process is generally not made, but without the assumption of evolution, we are sometimes told, cladistics is set adrift in a sea of "conceptual confusion" (Beatty, 1982: 33). Thus, according to Wiley (1981: 22), "the formalism of taxonomy must be subservient to the demands of evolution."

An alternative viewpoint about the relationship between cladistic analysis and evolutionary theory has surfaced within the last five years. Unfortunately, it has generated substantial misunderstanding, particularly outside the cladistic community, and consequently is worthy of a few words of clarification. More or less simultaneously, a number of workers proposed that there could be a separation between reconstructing historical pattern on the one hand and assumptions

about the process underlying that pattern on the other. These systematists suggested that the analysis of systematic pattern was (or certainly could be) independent of any preconceived notion of process (Gaffney, 1979; Eldredge, 1979; Platnick, 1979; Eldredge & Cracraft, 1980; Patterson, 1980, 1982a; Nelson & Platnick, 1981).

The reaction to transformed or pattern cladistics, as the above view has been called, has run from quiet acceptance to outright hostility. Most of the latter has originated outside cladistics itself (Beatty, 1982; Ridley, 1983) and has been founded more on its misunderstandings of cladistics than on any cogent criticism of pattern cladism (see responses of Platnick, 1982; Patterson, 1982b; Brady, 1982). Nevertheless, some potentially interesting issues are being raised by cladists themselves. For example, if a specific notion of evolutionary process is unnecessary, where does that leave our interpretation of the concept of synapomorphy? Phylogenetic cladists continue to view character transformation in terms of "primitive to derived sequences" and to argue that in constructing hypotheses of this transformation we must have some prior conception of historical relationships in order to undertake outgroup analysis. Pattern cladists might respond that synapomorphy is strictly a problem of deciding the level of generality of defining characters and that this can be arrived at by inspection and comparison of ontogenetic histories, thus eliminating the need for prior phylogenetic assumptions (see Nelson & Platnick, 1981; Rosen, 1984). The issue of which method of comparison (outgroup or ontogenetic) is primary, is an empirical matter to be decided by parsimony analysis, and indeed this is being debated at this time (Kluge, 1985; Brooks & Wiley, 1985; Nelson, 1985; Platnick, 1985). Matters of principle aside, in practice cladists from either side of the debate will use both ontogenetic and outgroup data to resolve systematic relationships, so perhaps in that regard the debate will not concern those systematists interested solely in cladistics as a methodological tool.

Although cladists might differ in their perceptions about the role of evolutionary assumptions within cladistics, as we noted earlier a shared set of common principles can be identified. To our knowledge, all pattern cladists believe in naturalism, whereby the hierarchical pattern of nature is assumed to be the result of naturalistic processes. Thus, to claim that pattern cladists do not believe in some form of "evolutionary" (historical) process behind phylogenetic pattern or that pattern cladistics is "antievolutionary" is simply mistaken. Pattern cladists merely claim that a prior commitment to a specific process is unnecessary in order to generate hypotheses about that pattern. And given that hypotheses about pattern have been proposed for hundreds of years, under different theoretical paradigms about the causes of that pattern (Patterson, 1977; Nelson & Platnick, 1981), their point seems to be well taken.

The Symposium

Speciation analysis. In the first paper, E. O. Wiley and R. L. Mayden show how the results of a cladistic study can be used to examine patterns and processes of speciation. Using species-level taxa within the eastern North American fish fauna, they begin by briefly discussing attitudes towards species concepts as they have been used by phylogenetic systematists. Wiley and Mayden then investigate patterns of relationships for numerous clades of fishes having common species borders of endemism. They show that these historical hypotheses inhibit intercladal congruence, which they then use as components of an analysis of speciation modes.

Historical biogeography. Donn Rosen begins his paper by addressing two widely held, but incorrect, assumptions: that fossils can tell us how old a taxon is, and that the ages of geologic events have been correctly assigned. He emphasizes the need for precision in specifying how historical biology is related to historical geology and shows how cladistics permits comparisons between these two systems. He seeks to discover patterns of congruence between historical biogeography and geological events so explicit that the congruence discovered cannot be dismissed as being due to chance or coincidence. Rosen stresses that it is the "independence of biological from geological data that makes the comparison of the two so interesting . . . ." He reviews Caribbean geologic history and presents a cladistic hypothesis for the historical interrelationships of the areas of that region. He points out that complex histories should lead us to expect complex patterns and that all potential hypotheses of area relationships may be corroborated by one or more cladistic patterns exhibited by the endemic taxa. Rosen also raises a warning for biogeographic analysis: in the past, some workers have assumed that dispersal is demonstrated by failure to discover

congruence in area relationships, yet even though dispersal may be widespread "theories of dispersal to explain biotic complexity are no more informative than theories of relationship based on symplesiomorphy . . . ."

Historical ecology and coevolution. Daniel Brooks discusses analytic methods of historical ecology and shows how they provide a missing component in studies analyzing the evolution of ecological associations. Direct estimates of ecological history are obtained by constructing cladistic hypotheses for as many interacting groups of organisms as possible. This method is contrasted with evolutionary ecology, which often uses indirect estimates such as the assumption that the age of ecological associations is proportional to its diversity. Using host-parasite data, Brooks addresses three questions within historical ecology: (1) How did species occurring in a given area come to be assembled? (2) How did two or more species having a close and evident ecological relationship come to be that way? And (3) Under what conditions did the ecological life history traits that we observe today emerge? Brooks shows how historical analysis through cladistics can provide insights into all of these ecological questions.

Hybridization. Vicki Funk addresses one of the major concerns of plant systematists, namely how to analyze hybridization within the context of a phylogenetic hypothesis. She summarizes the problems that arise during a cladistic analysis of a group whose taxa hybridize with one another, and she presents guidelines for interpolating hybrids into a cladogram. In order to exemplify these methods, she undertakes cladistic analyses of seven different genera exhibiting various degrees of hybridization among their component taxa. Funk stresses that all hypotheses regarding hybrid identification must be corroborated by chromosomal, distributional, and ecological data. A major conclusion is that cladistic analysis is indispensable when analyzing hybridization, but in cases of taxa exhibiting extensive hybridization, all systematic methods, including cladistics, may fail to give a clear indication of the history of the group.

Origin of the angiosperms. In the next paper, Peter Crane applies cladistic methodology to the question of the origin of the angiosperms. His central goal is to delineate the major groups of seed plants, to determine their interrelationships, and finally, to establish to which group of gymnosperms the flowering plants are most closely related. Crane accomplishes this task by providing an exhaustive analysis of extant and fossil groups of seed plants and establishes a framework within which competing theories of relationships are compared. By formulating the relevant phylogenetic questions more explicitly, he also provides an alternative to the established tradition of searching for ancestral groups.

Biological diversification theory. In the final paper, Joel Cracraft briefly describes the patterns of diversification that fall within the umbrella of a general theory of diversification. He proposes a hypothesis in which speciation rates are a function of the rate of change in large-scale geomorphological complexity, whereas extinction rates are a function of temporal and spatial changes in environmental harshness. Together, these two rate-controls describe a diversity-independent process of diversification. He then summarizes some of the evidence supporting this hypothesis, pointing out that the data themselves are often dependent upon knowledge of the phylogenetic relationships of many groups of organisms.

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SPECIES AND SPECIATION IN PHYLOGENETIC SYSTEMATICS, WITH EXAMPLES FROM THE NORTH AMERICAN FISH FAUNA[1]

E. O. WILEY AND RICHARD L. MAYDEN[2]

Phylogenetic systematics as developed by Hennig (1950, 1966) is a system of methods and a view of the world designed to integrate systematics with the evolutionary "paradigm." By evolutionary "paradigm" we mean the world view that organisms always have parents and that organismic diversity is a byproduct of descent with modification. If our view of phylogenetic systematics is correct, or even partly so, the results derived from Hennig's methods should be of general utility to the evolutionary community. We shall attempt to show this utility by considering how the results of phylogenetic analysis can be used to infer the mode of speciation involved in the origin of species. Before doing so, however, we need to discuss what constitutes a species because our concepts will influence our choice of units to be analyzed.

SPECIES IN PHYLOGENETIC SYSTEMATICS

There is no consensus concerning either the nature of species-as-taxa or the importance of species among those who align themselves with Hennig's (1966) basic philosophy. This should come as no surprise because no consensus on either question has been reached by the rest of the biological community. At the risk of oversimplifying, we will define two basic attitudes. The first is what might be called the heuristic attitude. Rosen (1979: 277) defined species as "a population or group of populations defined by one or more apomorphous features, it is also the smallest natural aggregation of individuals with a specifiable geographic integrity that can be defined by any current set of analytical techniques." Nelson and Platnick (1981: 11) stated "species are simply the smallest detected samples of self-perpetuating organisms that have a unique set of characters." Rosen's statement is somewhat more restrictive, both in its inclusion of a geographic criterion and in its criterion that the species must have at least one apomorphous character. Both, of course, are not "process free" concepts since one (Rosen's) contains a statement based on character evolution while the other (Nelson and Platnick's) contains a statement based on reproduction. Nevertheless, both concepts are as heuristic as the authors can make them.

The second attitude might be termed the "process" attitude. The concept applied is not restricted to purely heuristic considerations but also the evolutionary nature of the entities. Of all phylogeneticists, Hennig (1966) himself was the most radical proponent of this attitude, a fact that is not always appreciated. Hennig (1966) spent a substantial part of his book arguing against heuristic concepts because he rejected ideal morphology and the "morphological system." To Hennig (1966: 79–80), it was phylogeny that was important, morphology being a way of getting at the phylogeny:

> The categories [= taxa] of phylogenetic systematics are not constructed by abstraction. They are not defined as bearers of a complex of characters that remains if, starting with the individuals, we subtract more and more characters that are specific to the individuals and then to progressively more inclusive groups of individuals. In the phylogenetic system the categories [= taxa] at all levels are determined by genetic [= genealogical] relations that exist among their subcategories [= taxa included within them]. Knowledge of these relations is a prerequisite for constructing these categories [= taxa], but the relations exist whether they are recognized or not. Consequently here the morphological characters have a completely different significance than in the logical and morphological systems. They are not themselves ingredients of the definition of the higher categories [= taxa] *but aids* used to apprehend the genetic [= genealogical] criteria that lie behind them. [Brackets and emphases ours.]

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Thus Hennig (1) rejected taxa as being defined by characters and (2) accepted that the only characters useful to the phylogenetic system were those that indicated genealogical connections. Hennig wished to work with entities having a "real" existence in nature. Of course one consequence of holding to this realist view of the world concerned species—to Hennig species are important only to the extent that they function in the evolutionary process. Thus a concept of a species as a unit functioning in the evolutionary process was an important tenet in his system. For all practical purposes, Hennig (1966) adopted the concept that species are (or were at some stage) reproductive units, but differed from such workers as Mayr (1963) and Simpson (1961) in rejecting chronospecies. However, he did more than this. Hennig understood very clearly that species have many of the characteristics of individuals, especially singular places of origin in time and space (1966: 81):

> If we now attempt to evaluate the categories [= taxa] of the phylogenetic system from the viewpoint thus gained, there can be no doubt that all the supra-individual categories [= taxa], from the species to the highest category rank, have individuality and reality. They are all (. . .) segments of the temporal stream of successive "interbreeding populations." As such they have a beginning and an end in time (N. Hartmann), and there is a constant causal connection between the phases in which they are found at different times (Ziehen). All this is missing in the categories [= taxa] of the morphological or typological system, which consequently are timeless abstractions (Woodger) and therefore have neither individuality nor reality.

It would be a mistake to assume that his condemnation was directed only at paraphyletic and polyphyletic taxa.

Hennig was perfectly aware that species and natural higher taxa (i.e., monophyletic taxa) were not the same sorts of individuals as individual organisms. Michael Ghiselin isn't the same sort of individual as *Homo sapiens,* who isn't the same type of individual as Vertebrata. Further, he recognized that the concept of individuality provided a link in our understanding of the transition between species, higher taxa, and natural hierarchies (see Hennig, 1966: 82–83). Specifically:

> Thus all categories [= taxa] of the phylogenetic system are characterized by individuality and reality, in contrast to the abstract and timeless categories [= taxa] of the morphological system. This does not mean that they are all "individuals" in exactly the same sense as the individual organisms that are the units of life, and which we ordinarily call individuals. Depending on the purpose we have in mind, we may emphasize the common traits in the mode of existence of the individuals (in the customary, strict sense) and the supra-individual systematic groups, or we may emphasize the differences. But, we cannot transfer uncritically all the criteria of individuality that characterize one category rank [= taxa at one rank] to other category ranks [= taxa at higher or lower rank] if we are to avoid faulty conclusions (Hennig, 1966: 83).

Hennig went on to emphasize that his thoughts, apparently developed from considering Hartmann (1942, not seen, cited in Hennig, 1966), applied only to taxa that were natural in the phylogenetic sense.

Michael Ghiselin (1969, 1974, 1980, 1981) independently came to the same conclusion as Hennig (1966): particular species are individuals and most emphatically, they are not mere clusters, nor are they natural kinds. This distinction is discussed at length by Ghiselin (1969, 1974, 1980, 1981) and by Hull (1976, 1983). Natural kinds are held by many philosophers to be eternal, immutable, and discrete. The problem, pointed out by both Ghiselin and Hull, is that philosophers have traditionally thought of particular species as natural kinds, even after accepting that evolution renders particular species as temporary and changeable entities. We stress the phrase "particular species" because there is an additional confusing aspect to the problem—"species" refers to both particular species such as *Homo sapiens* and *Pinus ponderosa* and to a natural kind that defines a class of entities on which process operates: although *Pinus ponderosa* is changeable and temporary, the natural kinds "biological species" and "evolutionary species" are eternal and immutable. There may be no individual species that are the natural kind "biological species," but that doesn't mean there has never been such a species or that such a species will never appear in the future. The possibility of biological or evolutionary species is a permanent possibility, entities which fill the class

may evolve many times and in many places. An individual species, such as *Pinus ponderosa,* however, can evolve but once and once extinct is extinct forever.

PROCESS AND PATTERN IN SPECIATION

Speciation is one of the major processes underlying the patterns of descent that is the phylogeny of life on earth. As summarized by Wiley (1981) from many sources, speciation is not a single process but several more-or-less distinct processes that result in increases (and theoretical decreases) in the number of species in a clade. Patterns of genealogy at the level of species are the result of speciation. In some cases patterns of genealogy between clades are similar when examined in time and space. In other cases they are different. Different patterns may be the result of mistakes in reconstructing phylogenetic histories, the result of undetected extinctions or speciations, or the result of dispersals that alter the original pattern. These are all the result of our inabilities to detect what has actually happened. It is also possible that we have correctly reconstructed history and that the similarities and differences we observe in patterns of descent have a causal reason. Specifically, different modes of speciation might result in different patterns of genealogy in time and space. If so, and if we can couple differences of pattern with differences in mode, then we have additional tools with which we can gain a better understanding of the evolutionary process.

ASSUMPTIONS

Following the analysis of Wiley (1981) we shall explore the phylogenetic and biogeographic predictions derived from various proposed speciation modes that might be expected under certain conditions. The point of doing this exercise is to outline the conditions under which we can use genealogical and biogeographic information to determine which of the various modes might be operating. Obviously we do not expect all, or even most, groups to fulfill these conditions. At best we can hope that a few groups will fulfill the conditions and act as exemplars for studying the evolutionary process.

Assumption 1. Character evolution provides a reliable basis for inferring the history of speciation. There are two conditions under which this assumption would hold: (1) character evolution is coupled with speciation; or (2) character evolution keeps pace with lineage splitting, that is, there is enough anagenesis between lineage splits so that the sequence of splits leaves a "historical trail" that can be followed. Assumption 1 is violated if vicariance proceeds at a faster rate than character evolution, producing isolated populations that are similar. Subsequent evolution would not document the history of vicariance and a polytomy would result. (We shall see in a later section that a polytomy may exist even if character evolution does keep pace with vicariance.)

Two examples illustrate this. *Fundulus sciadicus* is composed of at least three disjunct populations (Fig. 1), presumably separated during the Kansan glaciation. If future divergent character change occurs before sympatry is achieved or before further splitting, a future phylogenetic reconstruction will not reflect the vicariance event involved. *Fundulus catenatus* is composed of at least five disjunct populations (Fig. 2), two of which might be correlated with the Ozark–Tennessee highlands vicariance event that we will discuss in a later section. Subsequent character evolution would not document the sequence of geographic isolation that this species has undergone.

Assumption 2. There are no extinctions of species in the clade. If we examine the results of particular speciation events, we must have some confidence that the species compared are the product of a single speciation event and not separated on the phylogenetic tree by several extinct, and unknown, species. If they are, then the differences observed may be the result of differences accumulated during several events. For example, *Fundulus parvipinnis* and *F. lima* are separated from other North American *Fundulus* by the Rocky Mountains and Great Basin. We know of fossil *Fundulus* from the Pliocene of California (Miller, 1945) and possibly from the Miocene of the Mohave Desert (Uyeno & Miller, 1963). Obviously ascribing the differences between Recent western *Fundulus* and their eastern counterparts to a single speciation event would be a dubious hypothesis. We simply don't know how many events were involved. The case of the *Fundulus nottii* species group (Wiley, 1977) is different. In this case (see Fig. 5 and discussion in a later section) there is no reason to believe that extinctions have occurred that would obscure the patterns because the group is distributed continuously over space.

Assumption 3. Dispersal has not obscured the original geographic pattern. Species pairs or clades that show large-scale dispersal may be identified

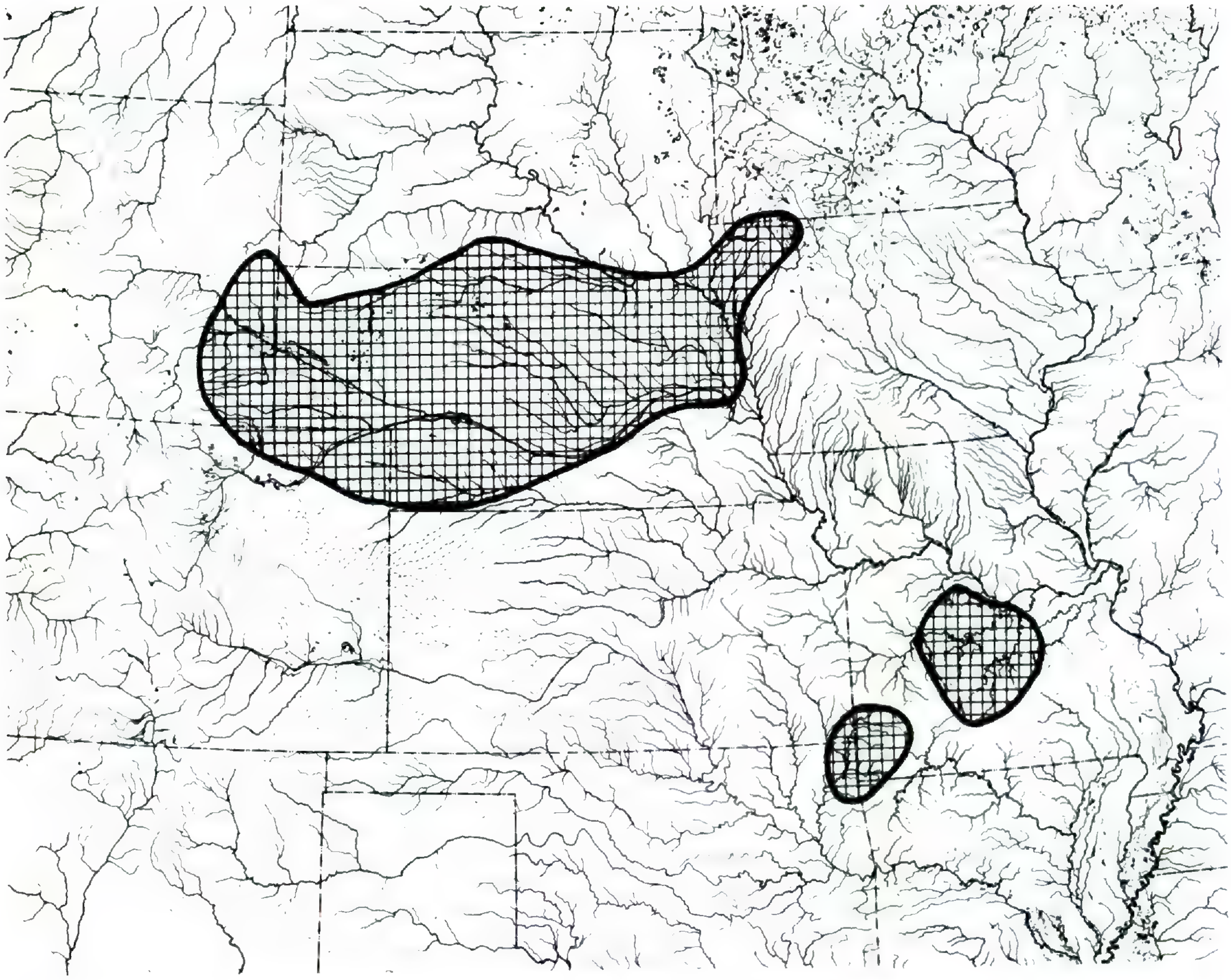

FIGURE 1. Distribution of *Fundulus sciadicus* (from Lee et al., 1980 and Ellis, 1914).

by widespread sympatry. For example, the pattern of speciation in the *Fundulus olivaceus* group (Fig. 3) is obscured by the widespread sympatry of *F. olivaceus* and *F. notatus* (Thomerson, 1966) and by the sympatry of *F. euryzonus* with both *F. notatus* and *F. olivaceus* (Suttkus & Cashner, 1981).

Obviously we cannot insure that any clade fulfills all three assumptions. However, we will suggest that some clades do because their histories and distributions show concordance with predictions based on particular modes of speciation and, in some cases, partial congruence in time and space with other groups. One final caveat—the modes we discuss are not our inventions and we have no interest in defending any of them as dominant or, in some cases, even realistic.

MODES AND PREDICTIONS

Following Mayr (1963), we may distinguish among three basic models of speciation. Reductive speciation involves lineage fusion; two species fuse to produce a third new species. While theoretically possible, there have been no documented cases of such events (Wiley, 1981). The nearest example would be a "compilospecies" (Harlan & deWet, 1963), in which one preexisting species simply absorbs the other. Additive speciation involves lineage splitting and reticulate speciation. The result is an increase in species diversity. There are several models for nonreticulate additive speciation that can be distinguished on the basis of the importance of geographic subdivision from essential (allopatric speciation) to nonessential (sympatric speciation). Additive speciation models are rich in predictions and we shall discuss several of them in sections below. The final model is "phyletic speciation," the proposition that there is species turnover within a single lineage without adding species in any one time frame. This "mode" has been rejected as a true mode of speciation by Hennig (1966) and by Wiley (1981) who pointed

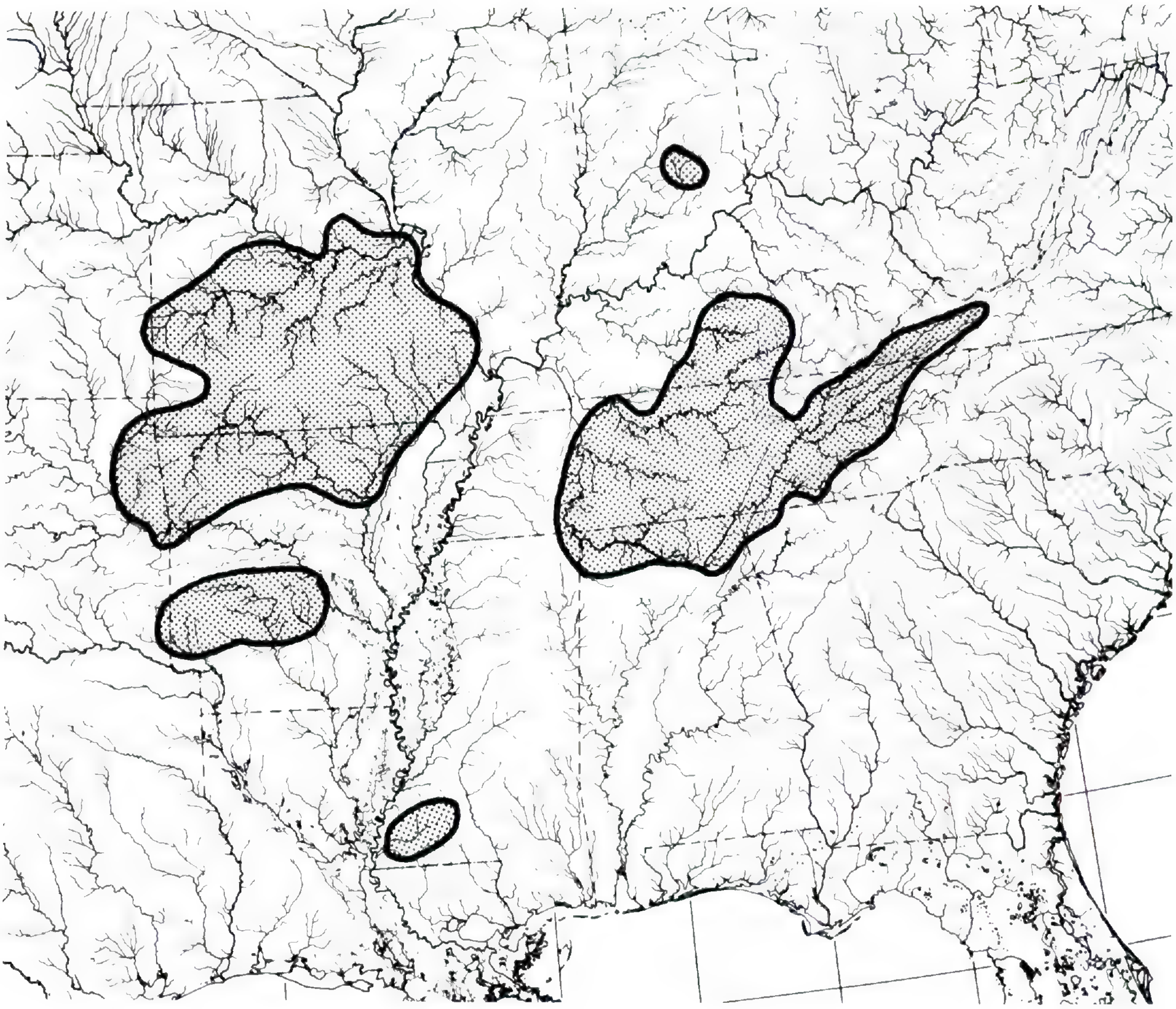

FIGURE 2. Distribution of *Fundulus catenatus* (from Lee et al., 1980).

out that subdividing a continuous lineage is an inherently arbitrary procedure. We shall not discuss it further.

ALLOPATRIC SPECIATION

Allopatric speciation is an umbrella term for a spectrum of modes that involve complete geographic separation of two or more subpopulations of a species during its evolution into two or more daughter species (one of which may be the ancestor itself). Allopatric speciation is thought to be the dominant mode by many investigators (cf. Mayr, 1963; Grant, 1971). Two basic models can be discerned based on population structure, a model that assumes gene flow is present and promotes lineage cohesion and one that assumes gene flow is absent or rare. The "gene flow model" can be further subdivided on the basis of the relative percent of the ancestral geographic range occupied by the subdivided populations. At one extreme we can envision equal partitioning of the ancestral range. At the other extreme we can envision the budding off of a very small part of the ancestral range, perhaps a single deme or even a single individual. Thus three models may be distinguished, two of which are extremes of a continuum.

ALLOPATRIC SPECIATION I—VICARIANCE

Vicariance speciation (Wiley, 1981) is a gene flow mode involving substantial geographic space. Differentiation may be manifested before geographic separation in the form of geographic variation, or it may not. Speciation may be rapid or slow depending on the amount of geographic variation existing before subdivision and the occurrence of evolutionary novelties after subdivision. Wiley (1981) suggested that the following phylogenetic and biogeographic predictions could be made based on this mode:

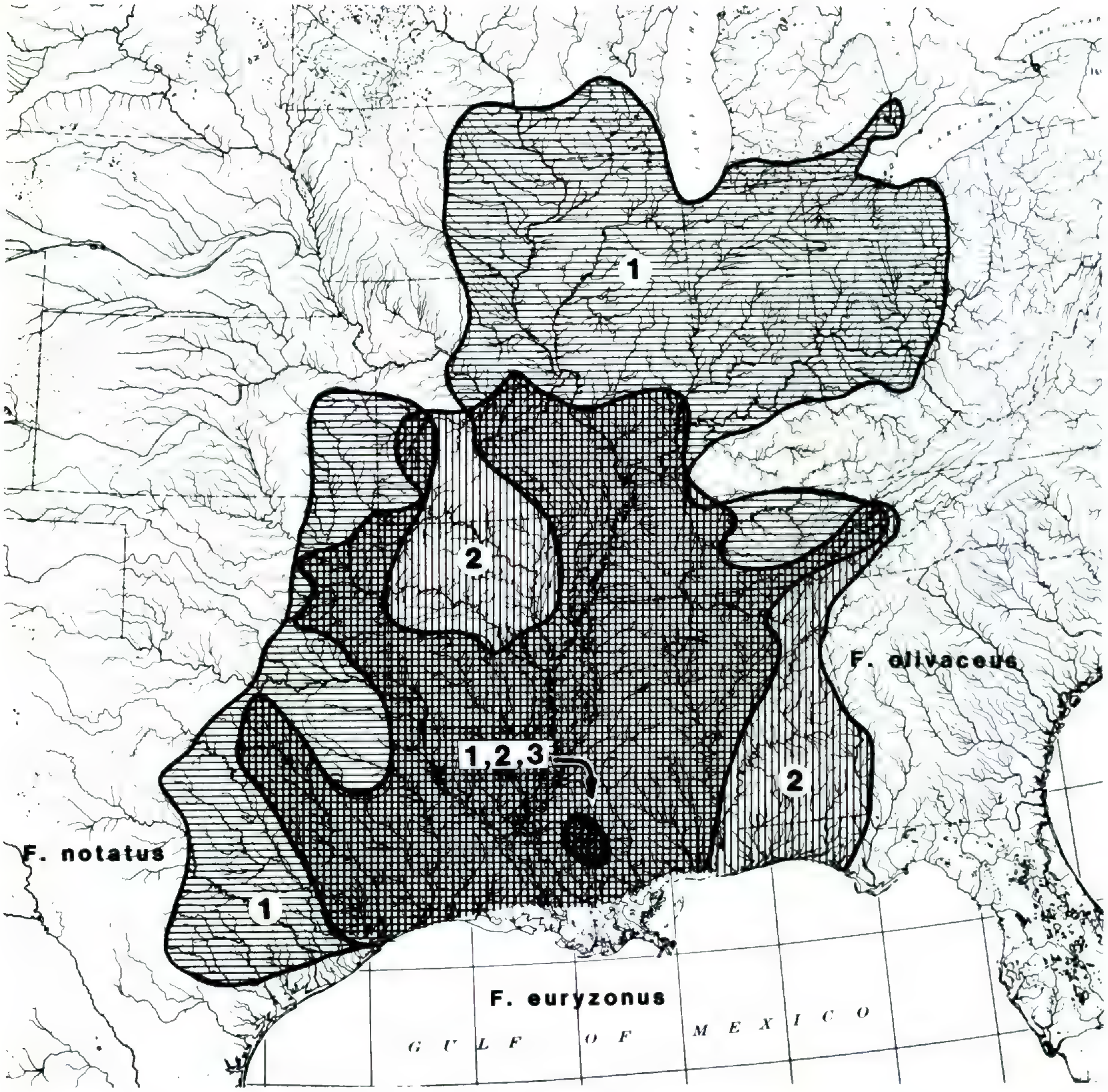

FIGURE 3. Distribution of the *Fundulus olivaceus* species group (from Lee et al., 1980 and Suttkus & Cashner, 1981).

1. Dichotomous phylogenies should predominate because of ancestral "extinctions," i.e., because there is no particular reason to think that either geographic subunit will be identical with the ancestor as a whole (Fig. 4).

2. The range of an ancestral species may be estimated by adding the ranges of daughter species.

3. Different clades should show common (congruent) patterns of speciation over time and space.

Predictions 1 and 3, dichotomy and some level of biogeographic congruence, are the important predictions. Of course, the congruence observed will be limited to those groups who (1) inhabit the same region, (2) are actually affected by the geographic event in question, and (3) have a history of character evolution that has kept pace with the subdivision.

Vicariance—Central Gulf Coast speciation. A number of clades of fishes contain sister species whose boundaries can be defined by the Mobile Bay drainage of the Central Gulf Coast of the U.S.A. Within the freshwater *Fundulus nottii* species group (Wiley, 1977; Fig. 5), *F. nottii* is found from streams draining into Lake Pontchartrain, Louisiana eastward to and including the lower reaches of the Mobile Bay drainage, Alabama. Its sister species, *F. escambiae*, is found from the Perdido River Drainage,

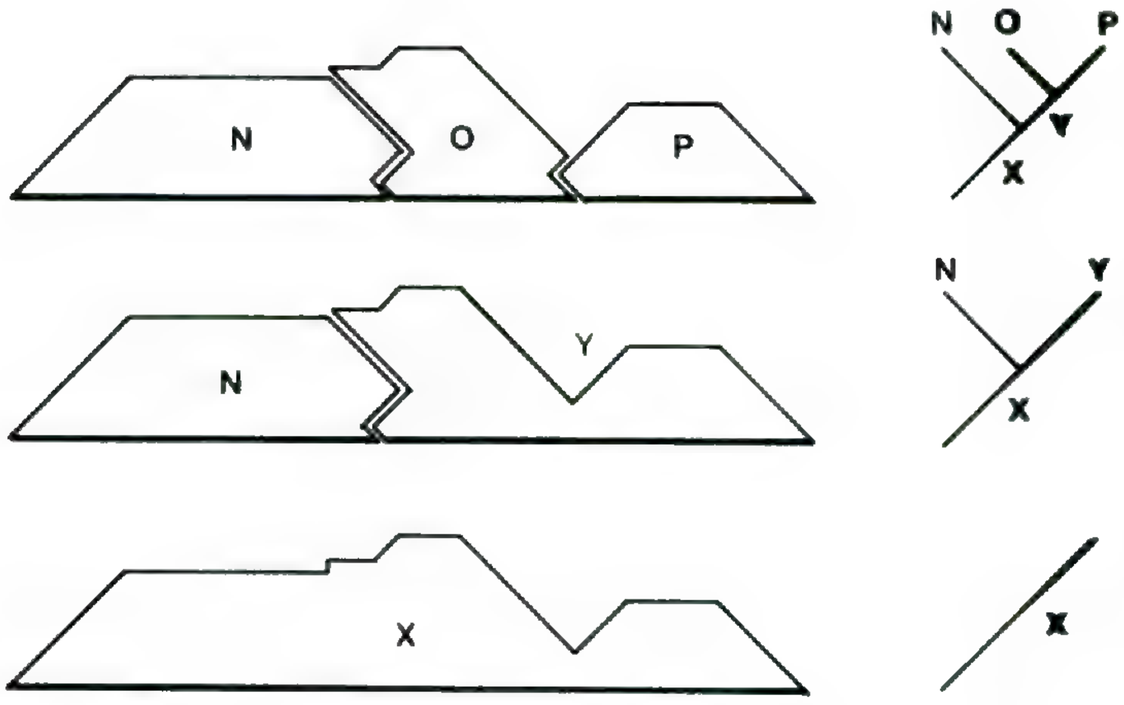

FIGURE 4. Speciation in the hypothetical clade NOP illustrating phylogenetic patterns expected in model 1 speciation.

Alabama to the lower Suwannee River, Florida. Phylogenetic analysis (Wiley, 1977) indicates that this species pair is most closely related to *F. lineolatus*, an Atlantic coastal species parapatric with *F. escambiae* (C. Gilbert, pers. comm.), and that the three together have affinities with the western sister pair *F. blairae–F. dispar* (see Fig. 5). There are several other fish groups showing a vicariant pattern at the Mobile Bay basin. These include:

1. *Fundulus confluentus* and *F. pulvereus* (Fig. 6), coastal and estuarine killifishes (Wiley, in press).

2. *Etheostoma chlorosomum* and *E. davisoni* (Fig. 7), freshwater darters (Howell, 1968; Page, 1983).

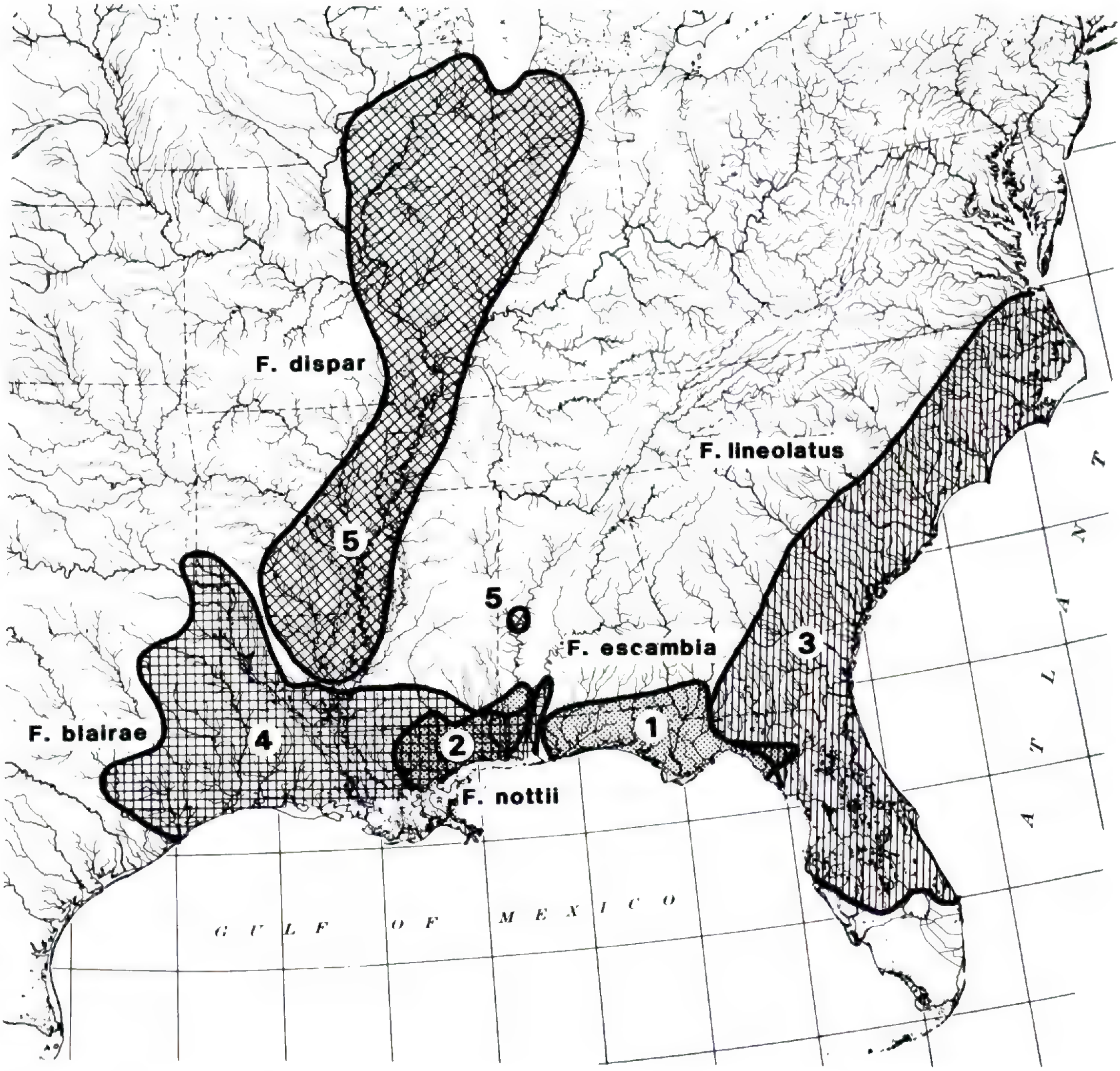

FIGURE 5. Distribution of the *Fundulus nottii* species group (from Wiley, 1977, with additional data from C. R. Gilbert, Univ. Florida). Tree: [4+5]+[3+(1+2)]. Characters supporting tree: see Wiley (1977, in press).

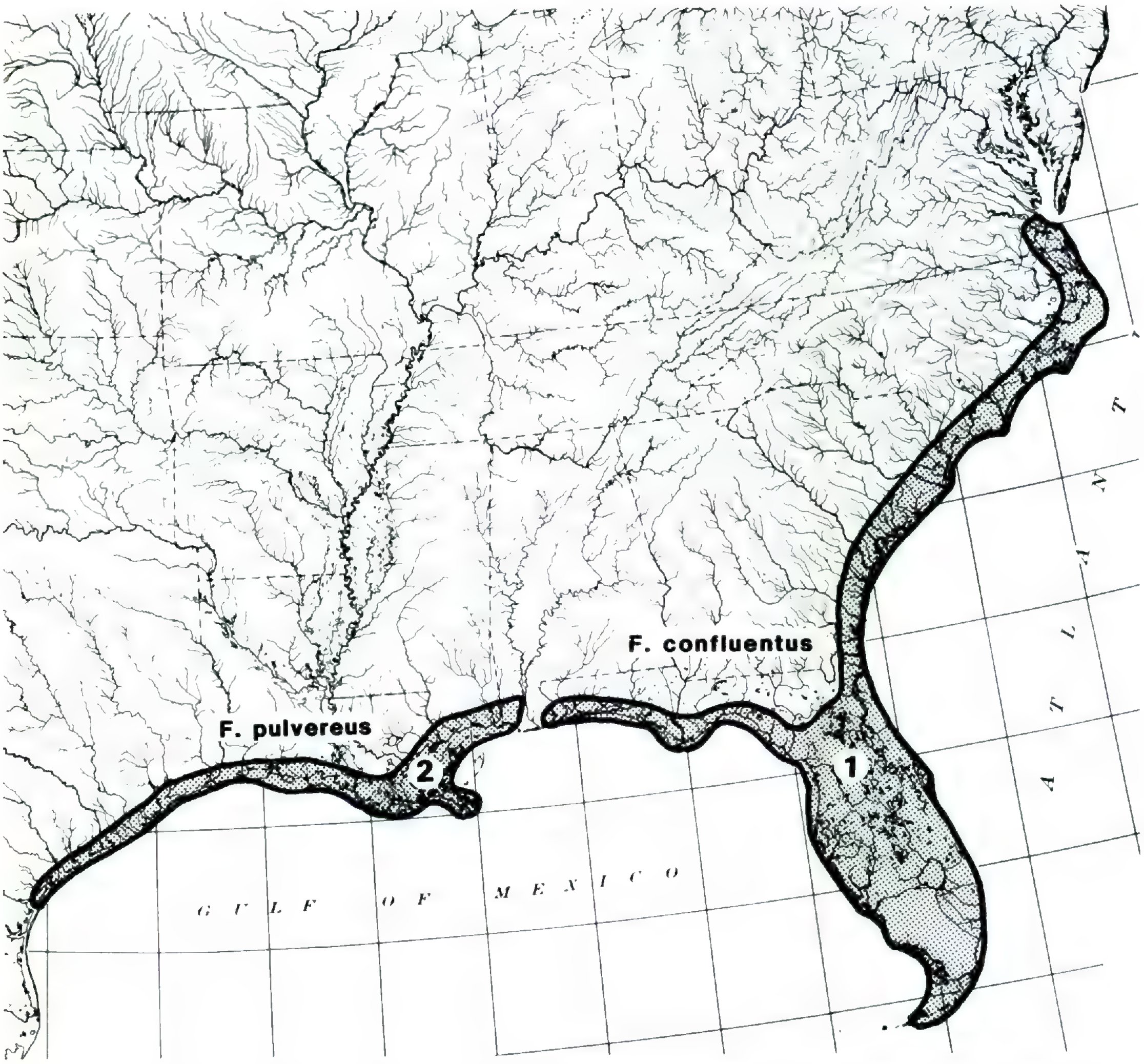

FIGURE 6. Distribution of *Fundulus confluentus* and *F. pulvereus*. (Reylea, M.S. Thesis, Florida State Univ., 1965, recognizes most Atlantic populations north of Florida as belonging to *F. pulvereus* and he recognizes a zone of intermediates between the Apalachicola River and Mobile Bay. We do not follow this, but we recognize the need for further study.)

3. *Ammocrypta beani* and *A. bifasciata*, freshwater sand darters (Fig. 8; from Williams, 1975).

4. *Hybopsis winchelli* and an undescribed species (Fig. 9), freshwater chubs (Clemmer, 1971; Lee et al., 1980).

In addition, several groups of snakes show vicariant patterns along the Mobile Bay basin, some on the level recognized as species, some as subspecies. These include:

1. *Nerodia rhombifera* and *N. taxispilota*, water snakes (Fig. 10; Mount, 1975).

2. Two subspecies of *Nerodia cyclopion* (Fig. 11; Mount, 1975).

3. Two subspecies of *Farencia abacura*, the mudsnake (Fig. 12; Smith, 1938; McDaniel & Karges, 1983).

Additional possible examples of this pattern also exist, but are complicated by the presence of a Mobile Bay drainage endemic, borders which do not exactly correspond to the event, dispersal, or the lack of an adequate phylogenetic hypothesis. These include:

1. *Notropis longirostris* and an undescribed species, two shiners, with the undescribed species endemic to the Mobile Bay drainage and *N. longirostris* found both east and west (Fig. 13; Swift, 1970; Lee et al., 1980; R. D. Suttkus, pers. comm.).

2. The *Notropis roseipinnis* species group,

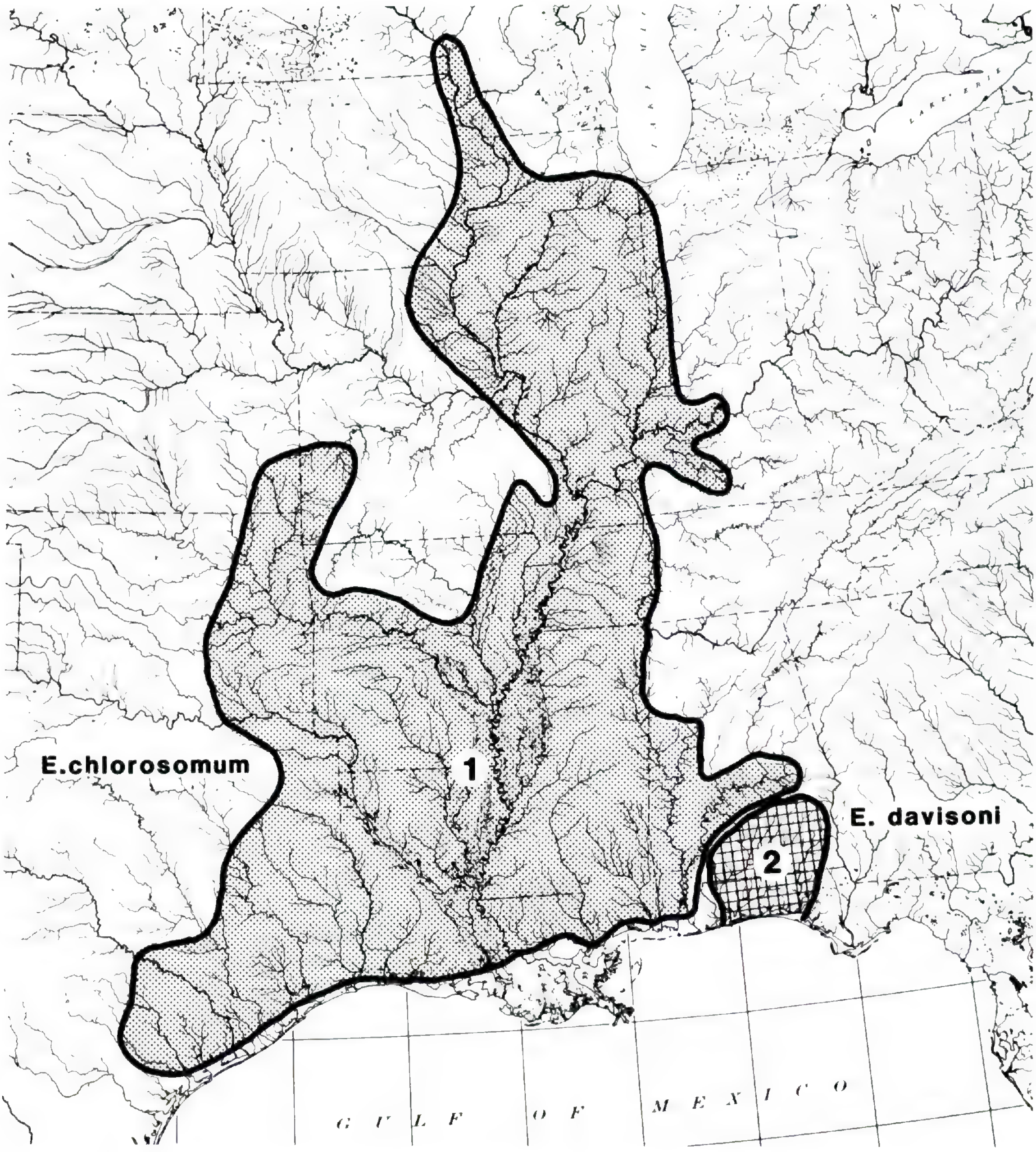

FIGURE 7. Distribution of *Etheostoma chlorosomum* and *E. davisoni* (from Page, 1983).

three shiners, with the Mobile endemic being the sister of the species *east* of the Mobile rather than west (Fig. 14). Snelson (1972) presented different possible phylogenies of these species and recently Stein et al. (1985) considered the above relationships to be most parsimonious.

3. *Ammocrypta meridiana,* a Mobile Bay endemic, is the sister species of the *A. vivax–A. pellucida* species group (Fig. 15; Williams, 1975; Page, 1981). This pattern is similar to that of the *Notropis roseipinnis* group and has a Mobile endemic, but differs from it and the *F. nottii* group in lacking a species east of the Mobile.

4. The *Notropis hypselopterus* species group in which there is an apparent peripheral isolate, *N. euryzonus,* closely related to the eastern species *N. hypselopterus.* The western species, *N. signipinnis,* shows a broad area of sympatry east of the Mobile (Fig. 16; Bailey & Suttkus, 1952; Suttkus, 1955; Gilbert & Platania, 1980).

5. *Percina sciera* and *P. nigrofasciata* (Fig. 17) show a pattern opposite of the *Notropis hypselopterus* group with the eastern species being widely sympatric with its sister *west* of the Mobile. This is further complicated by having two additional species (*P. aurolineata* and *P. lenticula*) of this clade in the middle of the distributional pattern of the clade (Lee et al., 1980; Page, 1981).

6. Two species of the turtle genus *Sternotherus, S. carinatus* and *S. minor,* show a pattern that might have resulted from a vicariance event involving the Mobile Bay drainage, but the pattern is complicated by the presence of *S. minor* in the Pearl River drainage of Mississippi and Louisiana (Fig. 18; Tinkle, 1958).

7. Two subspecies of the cottonmouth, *Agkistrodon piscivorus* (Fig. 19; Conant, 1975), two races of kingsnakes, *Lampropeltis getulus,* and two races of the pinesnake, *Pituophis melanoleucas,* have borders that correspond to a Mobile Bay vicariance (Mount, 1975) but in each case there are additional races or subspecies and there are no phylogenetic hypotheses demonstrating that the races with borders at the Mobile Bay drainage are closest relatives.

Another group of species show evidence of a more western vicariance event loosely associated with the Mississippi River. Within the *Fundulus nottii* species group, *F. blairae* and *F. dispar* are largely confined to the western part of the range (Fig. 5) and are the sister group of the eastern members of the group. A similar pattern is seen in *Ammocrypta,* with *A. clara* being the sister species of the *beani–bifasciata* species pair (Fig. 8). Additional examples might include:

1. *Notropis sabinae,* the sister species of the *N. longirostris* complex (Swift, 1970; Coburn, 1982; Fig. 13).

2. *Notropis umbratilis–N. ardens* species pair, sister group of the *N. roseipinnis* group (Snelson, 1972; Mayden, unpubl. data; Fig. 14).

Other groups may show a similar pattern, but the phylogenetic relationships among the members have not been investigated. These include:

1. Two subspecies of the turtle *Deirochelys reticularia* (Fig. 20; Zug & Schwartz, 1971), but there is a third subspecies.

2. "*Notropis*" *amnis* and the *Hybopsis amblops* complex (Fig. 9), but there are at least five species inhabiting other regions whose relationships are not known (Clemmer, 1971; Coburn, 1982; Mayden, unpubl. data).

In summary, there are possibly two large-scale vicariance events on the Northern Gulf Coast, one splitting the areas east and west of the Mobile Bay drainage and one involving the areas east and west of the Mississippi River. For those groups that show both patterns, it appears, based on the phylogenies, that the vicariance centering around the Mississippi is older than that centering around the Mobile Bay.

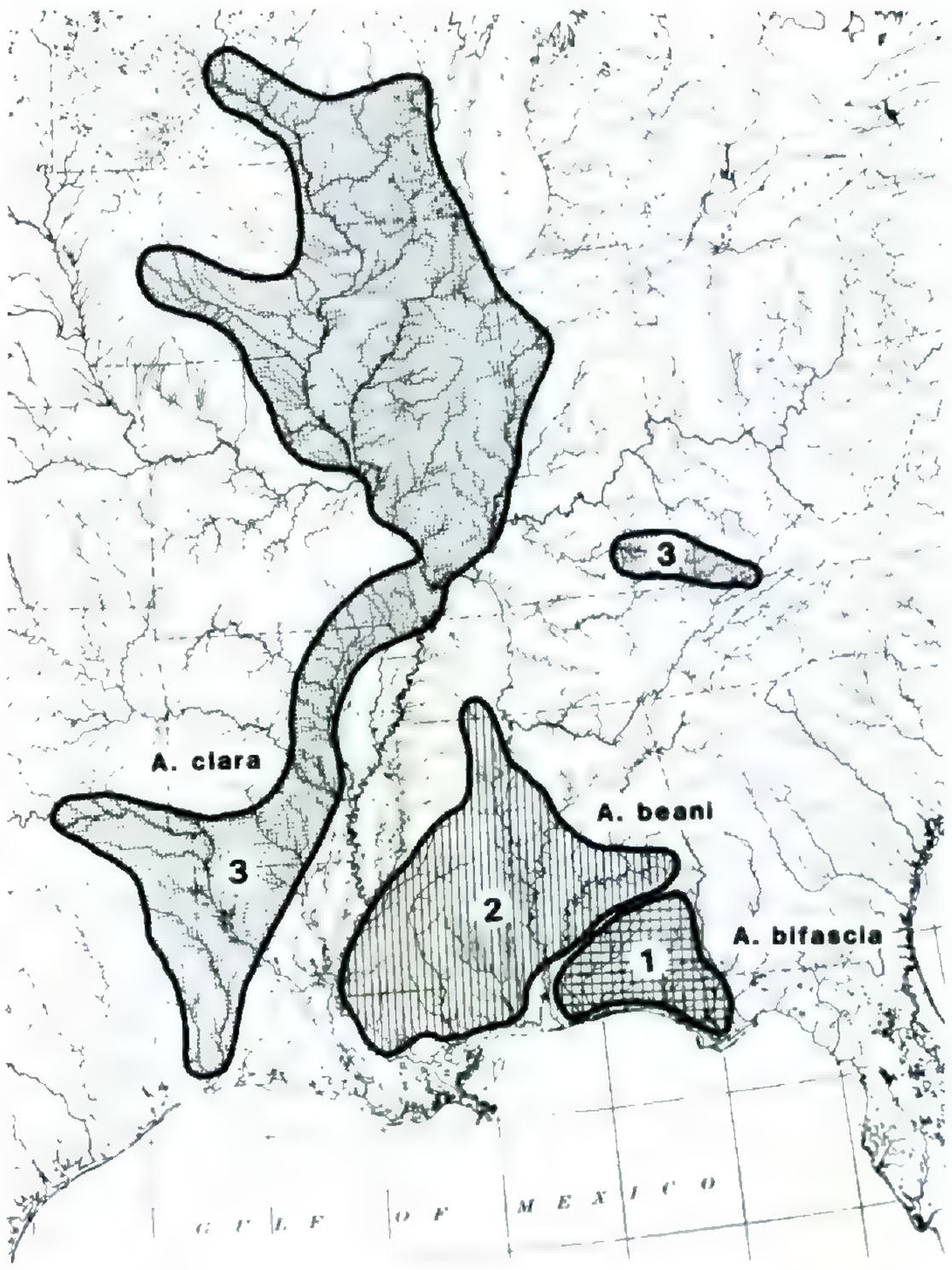

FIGURE 8. Distribution of the *Ammocrypta beani* species group (from Williams, 1975). Tree: 3+(1+2). Characters supporting tree: see Williams (1975).

Vicariance—the Central Highlands. The Central Highlands of the U.S. may be broadly conceived of having two major components. The Interior Highlands comprises the Ozark Plateau and Ouachita Highlands. The "Tennessee Highlands" comprises the Interior Low Plateau, the Ridge and Valley Province, and the Blue Ridge Province—essentially that part of the Central Highlands drained by the Ohio, Tennessee, and Cumberland Rivers between the Appalachian Divide and the Coastal Plain. The faunas of interest are largely confined to high gradient streams, which usually have clear waters and rocky bottoms. Both areas have faunal (and no doubt floral) endemics and the closest relative(s) of an endemic in one area is likely to be found in the other area. In Figure 21, we have plotted

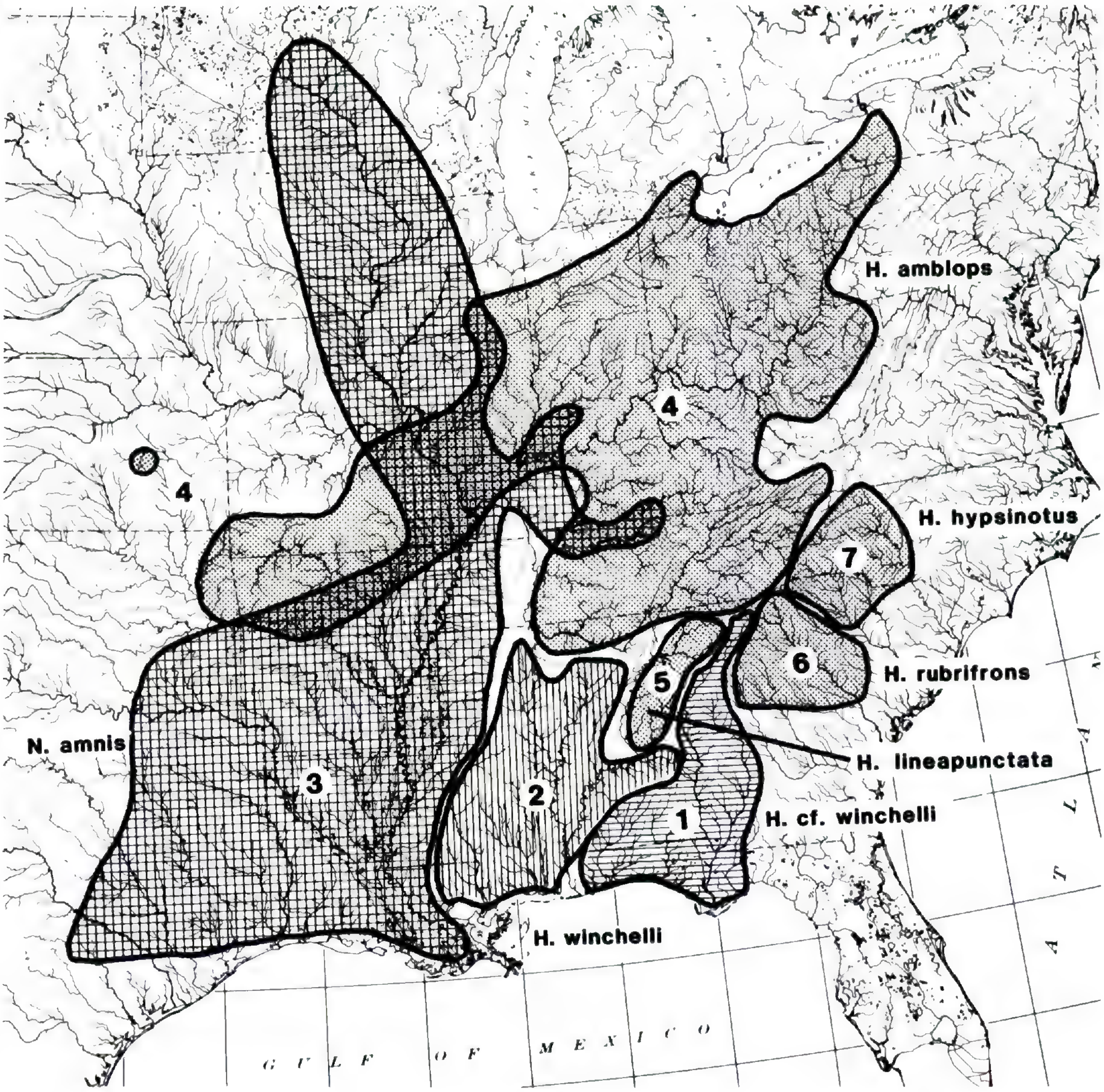

FIGURE 9. Distribution of *Hybopsis amblops* and related species (from Lee et al., 1980). Tree: (1+2)+3+4+5+6+7. Characters supporting the monophyly of the group: (1) oval orbit, (2) prominent lateral spines on the neck of the urohyal, (3) broad parasphenoid, (4) long neck on first basibranchial, (5) enlarged first pair of hypobranchials, and (6) elongate interhyal (Mayden, unpubl. data).

the total ranges of 44 species of freshwater fishes whose ranges are largely confined to one or both regions of the Central Highlands. (The many areas plotted north of these regions define various disjunct populations of species found in the region.) Not shown on this map, but plotted on subsequent maps are the ranges of close relatives outside the Highlands. Further, we do not show or discuss the large numbers of species endemic to various areas of the Tennessee or Ozark Highlands. The southern boundaries of the majority of the species shown in Figure 21 are largely congruent and form a border with the margins of the Cretaceous sea coincidental with the Coastal Plain. The northern boundaries of the Central Highlands fauna are not distinct owing to numerous disjunct populations of species otherwise confined to the two regions.

Geologic data indicate that prior to the Pleistocene many of the streams of Ohio, Indiana, and Illinois were high gradient and thus suitable for highland fishes (Thornbury, 1967; see Mayden, 1985, for summary). Further, drainage patterns were different, and what is now loosely referred to as the "Central Lowlands" was a highland region prior to the Pleistocene. Much of the

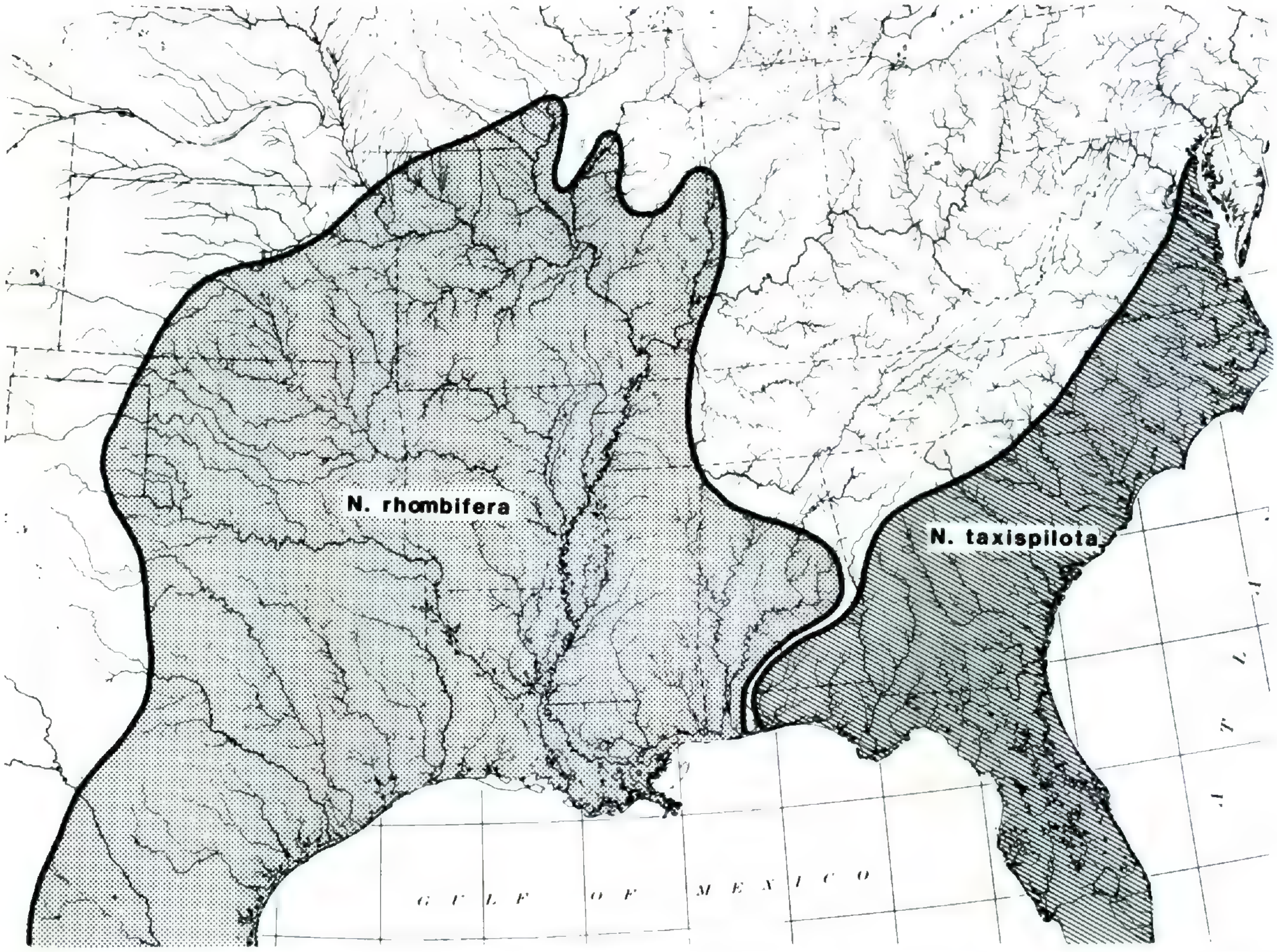

FIGURE 10. Distribution of *Nerodia rhombifera* and *N. taxispilota* (from Mount, 1975 and Conant, 1975).

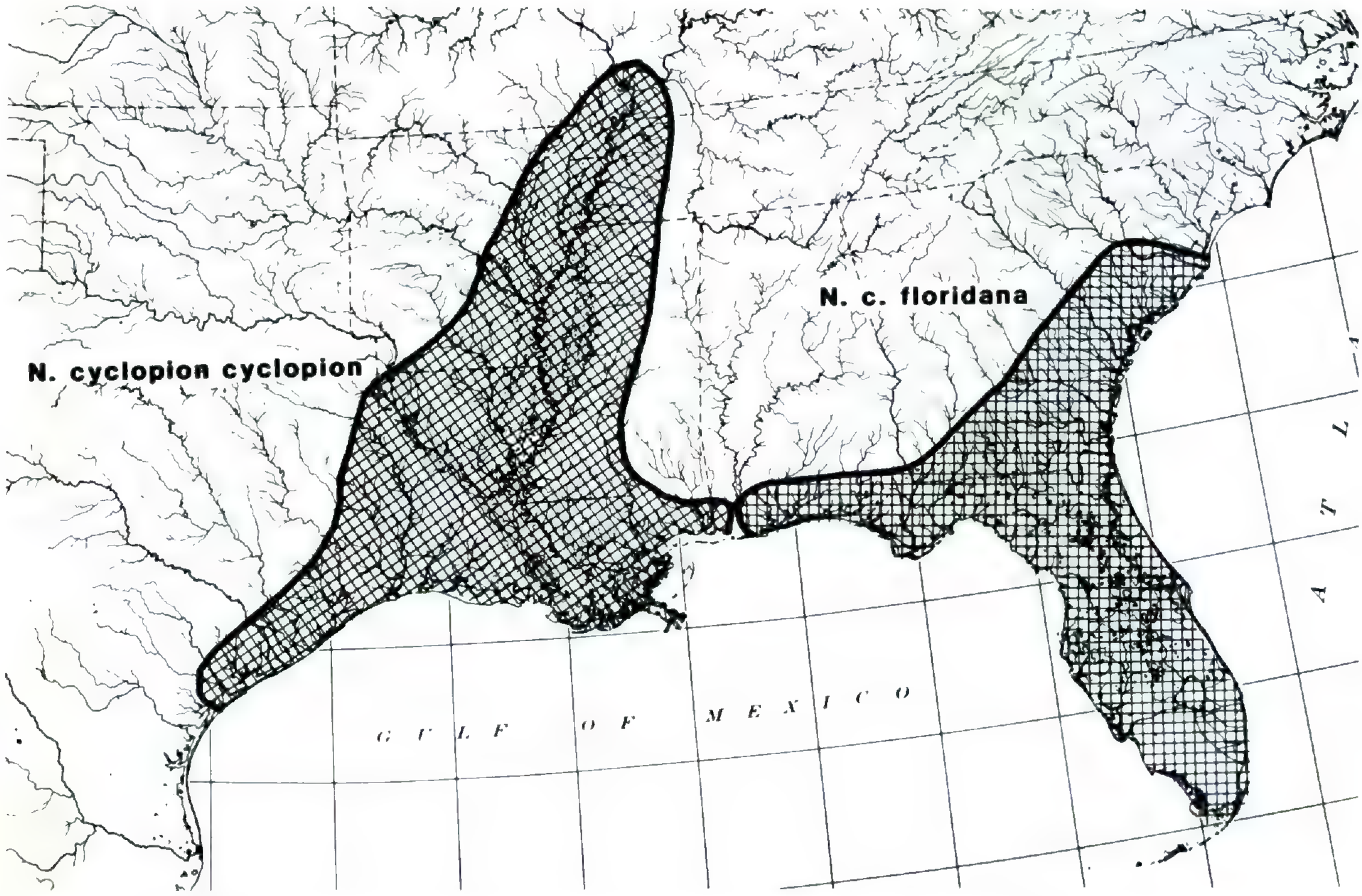

FIGURE 11. Distribution of two subspecies of *Nerodia cyclopion* (from Mount, 1975 and Conant, 1975).

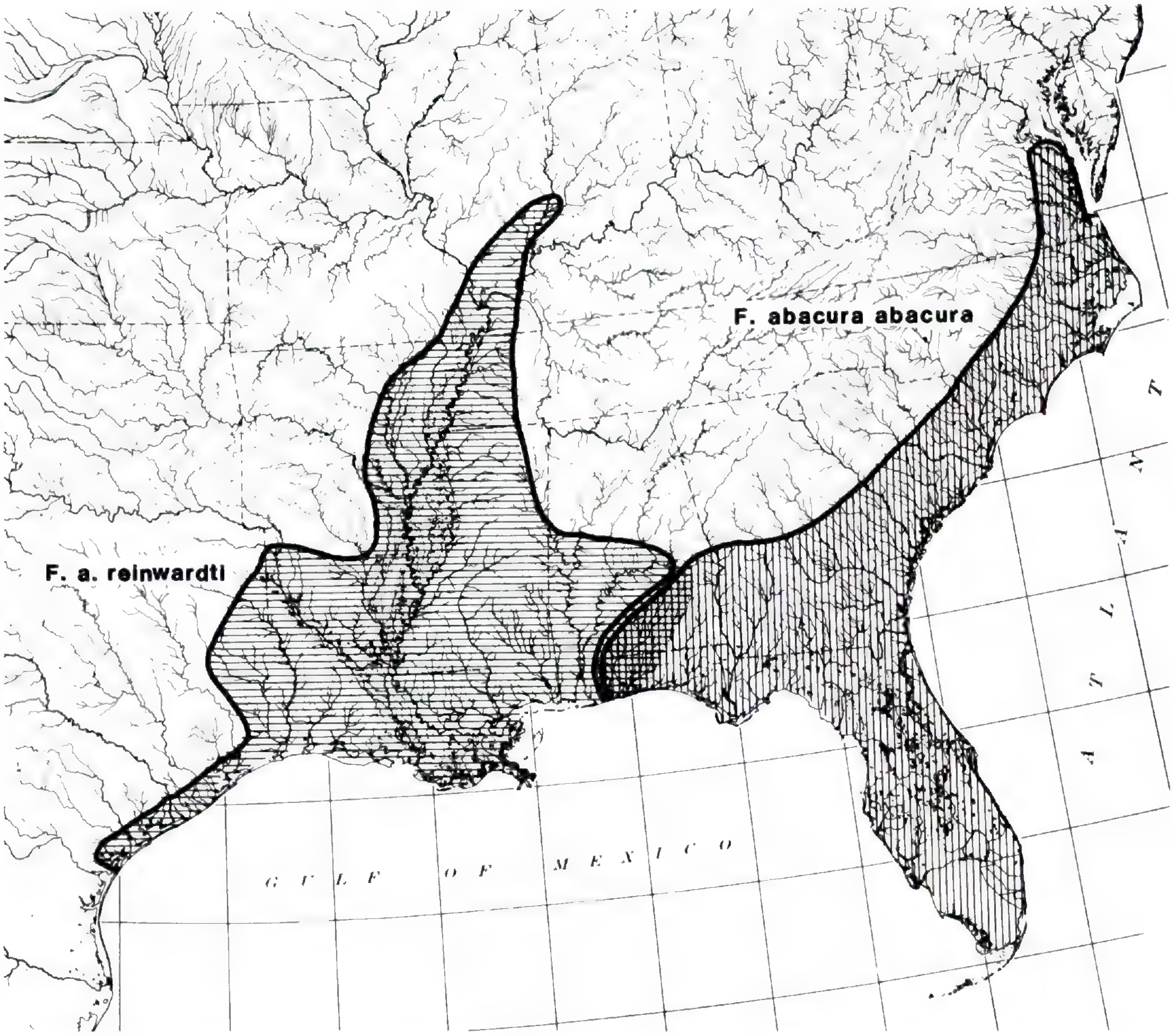

FIGURE 12. Distribution of two subspecies of *Farencia abacura* (from Smith, 1938 and McDaniel & Karges, 1983).

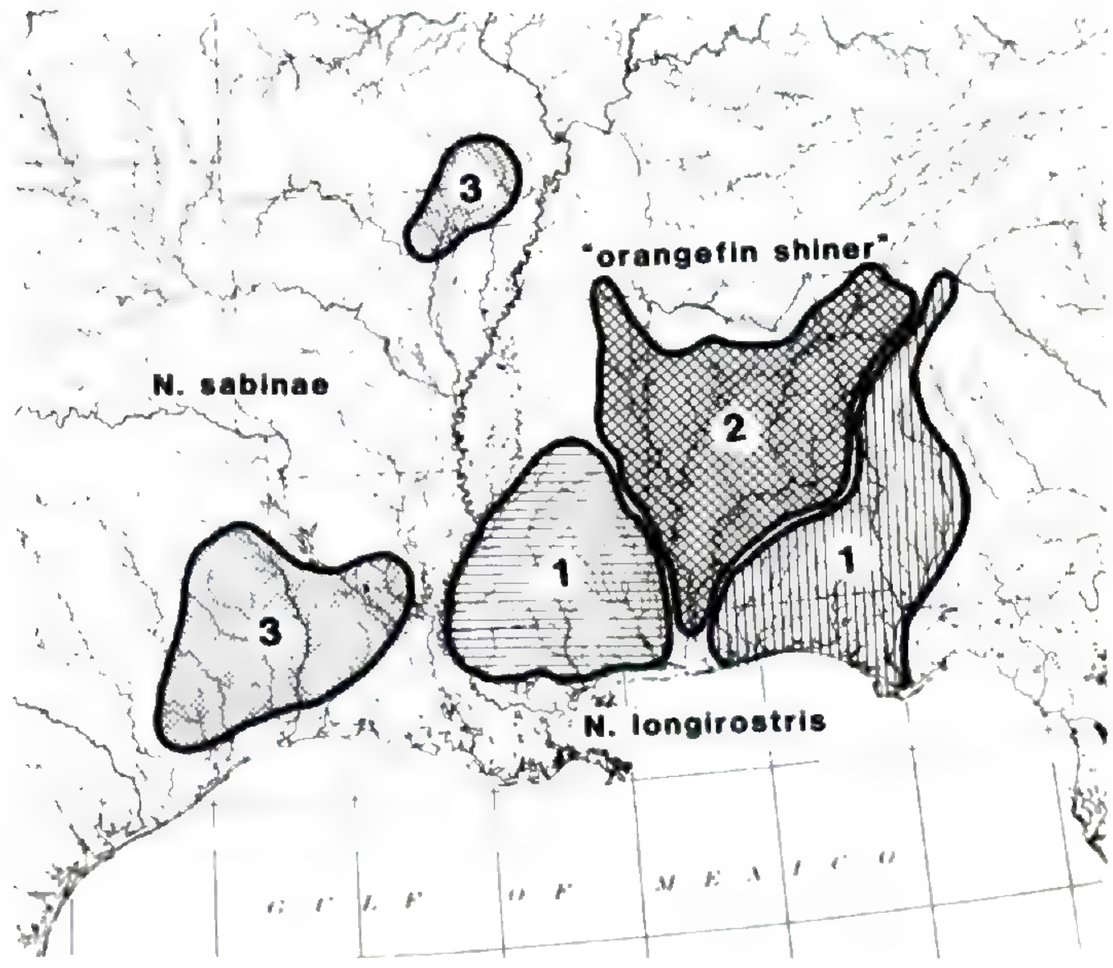

FIGURE 13. Distribution of the *Notropis longirostris* group (from Lee et al., 1980 and R. D. Suttkus,

Tennessee Highlands was drained by the Teays River (labeled 9 in Fig. 22) that joined the Mississippi north of St. Louis. To the south the old Ohio (labeled 10 in Fig. 22) joined with the Cumberland to empty directly into the Mississippi and did not join with the Tennessee (see Hocutt et al., 1978, for a review). The present drainages are a consequence of Pleistocene phenomena. Thus, prior to the Pleistocene there is evidence that (1) the highland fauna covered a more extensive geographic area than today and (2) the drainage patterns were much different.

←

pers. comm.). Tree: 3+(1+2). Characters supporting monophyly of the group: (1) maxillary process of palatine elongate and anteriorly directed, and (2) enlarged plate-like second infraorbital (Mayden, unpubl. data). Characters uniting (1+2): see Swift (1970).

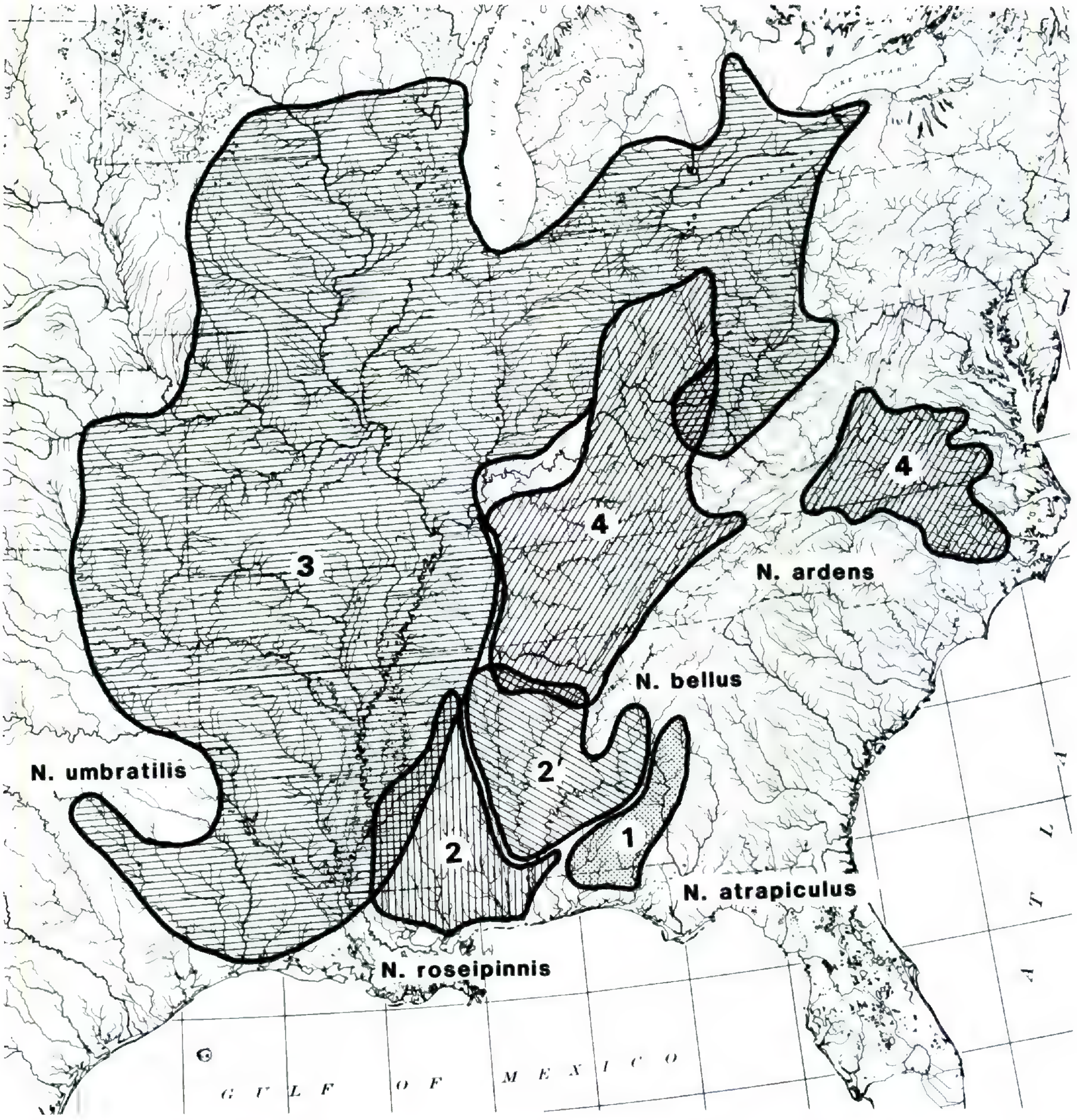

FIGURE 14. Distribution of the *Notropis roseipinnis* species group (from Lee et al., 1980). Tree: [3+4]+[2+(1+2′)]. Character uniting the group: breeding colors of males consisting of bright blues and reds (Mayden, unpubl. data). Character uniting (3+3): dark vertical bars on dorsum of breeding males (Mayden, unpubl. data). Relationships of [2+(1+2′)] are discussed in Stein et al. (1985).

The distinctiveness of the Central Highlands is partly reflected by the presence of species largely endemic to both areas. Among these are the minnows *Notropis galacturus* (Fig. 23) and *N. boops* (Fig. 24), the extinct sucker *Lagochila lacera* (Fig. 25), and cavefish *Typhlichthys subterraneus* (Fig. 26), the darter *Percina evides* (Fig. 27), and the salamander *Eurycea lucifuga* (Fig. 28). The distinctiveness of each region is also reflected by the presence of numerous endemic species that are not considered in this analysis.

When we presented data at the symposium concerning the Central Highlands fauna we thought that speciation within the clades inhabiting these regions might be due to Pleistocene glaciation. Glacial activity caused the regions to the north to become disjunct by depositing till and/or loess and silting of the streams in areas now referred to as the Central Lowlands. This might be termed the "Pleistocene hypothesis." The question is not whether the Illinoian (and probably the earlier Kansan) Glacier caused a

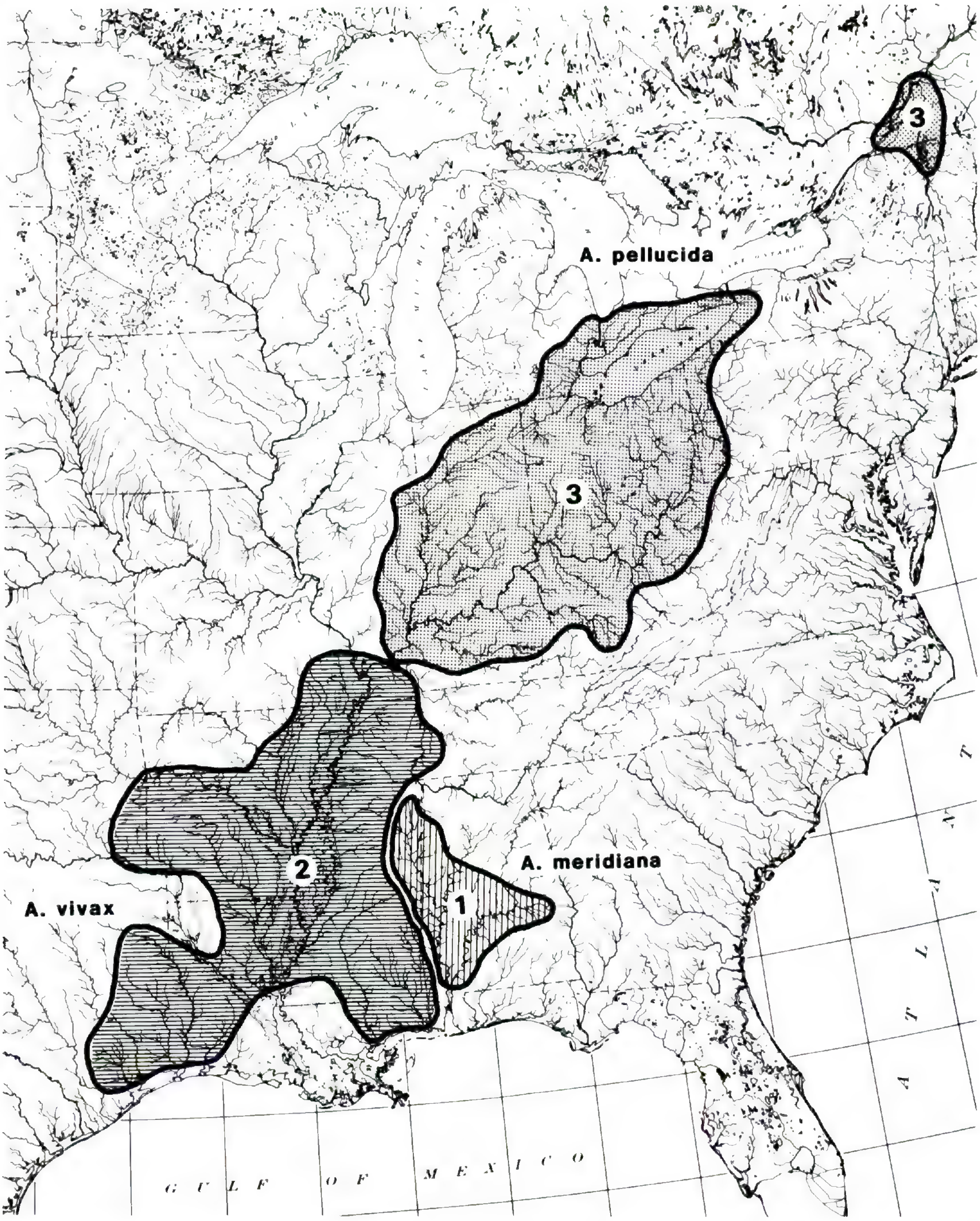

FIGURE 15. Distribution of the *Ammocrypta pellucida* species group (from Williams, 1975). Tree: 1+(2+3). Relationships discussed by Williams (1975).

disjunction. Rather, was some of the speciation within the Central Highlands fish fauna correlated with the event(s) or, were the species we observe today extant at the beginning of the Pleistocene and perhaps speciated, in a drainage system pattern that was subsequently replaced by the pattern we see today? This latter hypothesis might be termed the "pre-Pleistocene hypothesis."

Clades that conform to the Pleistocene hypothesis would be expected to show the following attributes: (1) they have one speciation event that

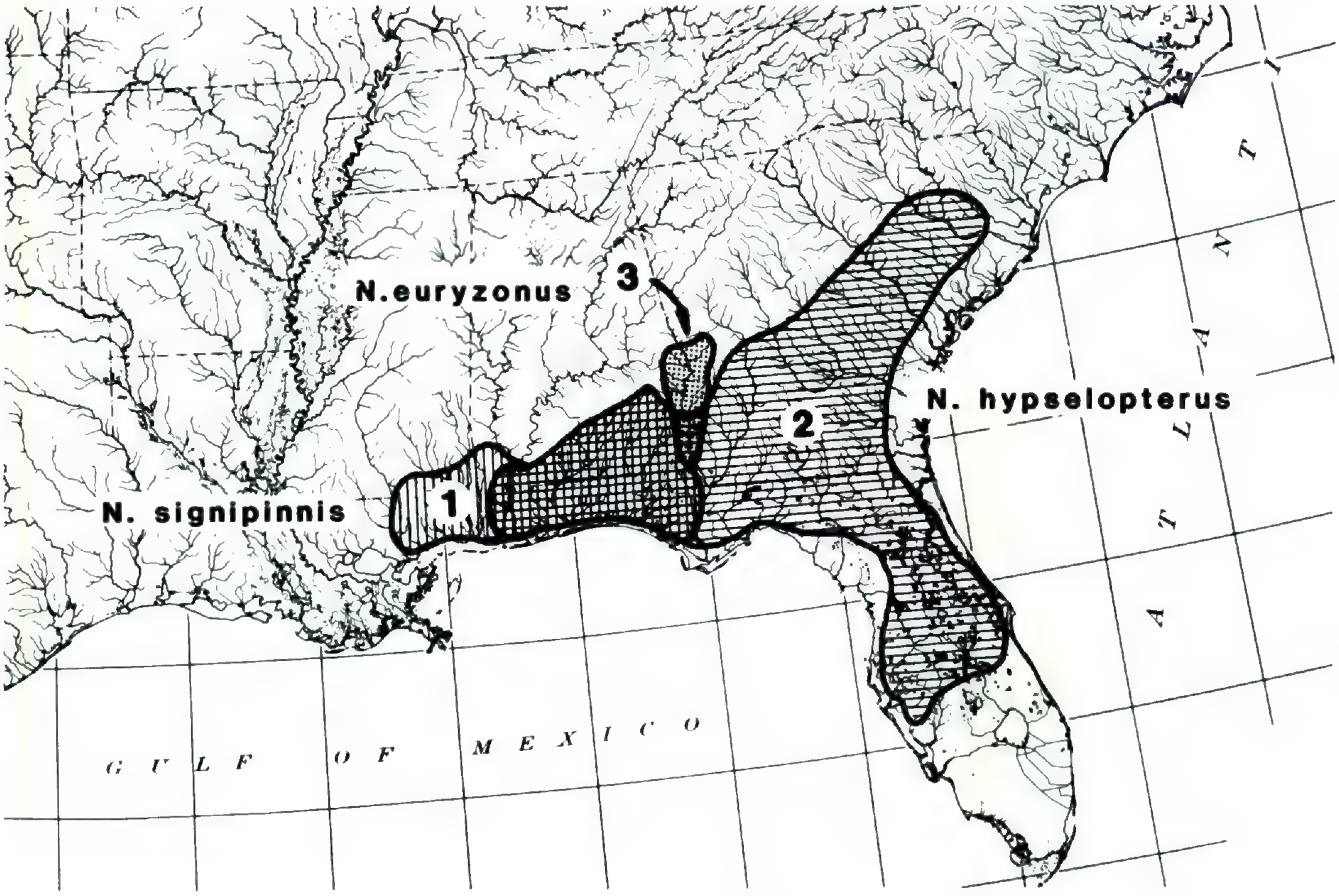

FIGURE 16. Distribution of the *Notropis hypselopterus* species group (from Gilbert & Platania, 1980). Tree: 1+(2+3). Characters supporting monophyly of the group: (1) very shallow preethmoid socket on the palatine, (2) presence of a broad lateral stripe on the body, and (3) iridescent colors (Mayden, unpubl. data). Characters supporting (2+3): breeding tubercles on mandibles directed laterally and in "comb" rows (Mayden, unpubl. data).

is congruent with the Interior-Tennessee disjunction, and (2) no speciation event within either region can be correlated with an event that was pre-Pleistocene or pre-Illinoian in origin. Three species groups conform to these attributes:

1. The *Notropis spectrunculus* species group (Fig. 29). A clade of two described and one undescribed species (Ramsey, 1965; Mayden, unpubl. data). Only the described species ranges are shown, the undescribed species is found in the Tennessee and Cumberland River systems and is the sister species of *N. spectrunculus* (Branson, 1983).

2. *Etheostoma niangue* and *E. saggita* (Fig. 30). Most workers (e.g., Bailey, 1948; Page & Whitt, 1973) have considered this pair sister species. Relationships to other members of the genus are not clear.

3. *Percina cymatotaenia* and *P.* sp. cf. *cymatotaenia* (Fig. 31) (Page, 1974, 1983).

This is not an impressive list. Further all three clades show wide geographic disjunctions between species that indicates much extinction and, in no case do we have the phylogenetic information necessary to relate any of these clades to other species within their genera. Finally, while they conform to our expectations regarding the Pleistocene hypothesis, they are also perfectly consistent with the pre-Pleistocene hypothesis.

Clades that conform to the pre-Pleistocene hypothesis may be expected to show the following attributes. (1) They contain one or more species in both the Interior and Tennessee Highlands and one or more additional species endemic to one of these regions, indicating that speciation in the clade and the achievement of sympatry occurred before the Pleistocene. (2) They contain a species (or more than one species) that has relict populations of early Pleistocene origin, dating that species as existing before Illinoian glaciation, the last known event to split the Central Highlands. (3) They contain species whose origin can be dated as early Pleistocene or pre-Pleistocene and who are of more recent origin than the taxa conforming to the disjunction between the Tennessee and Interior Highlands.

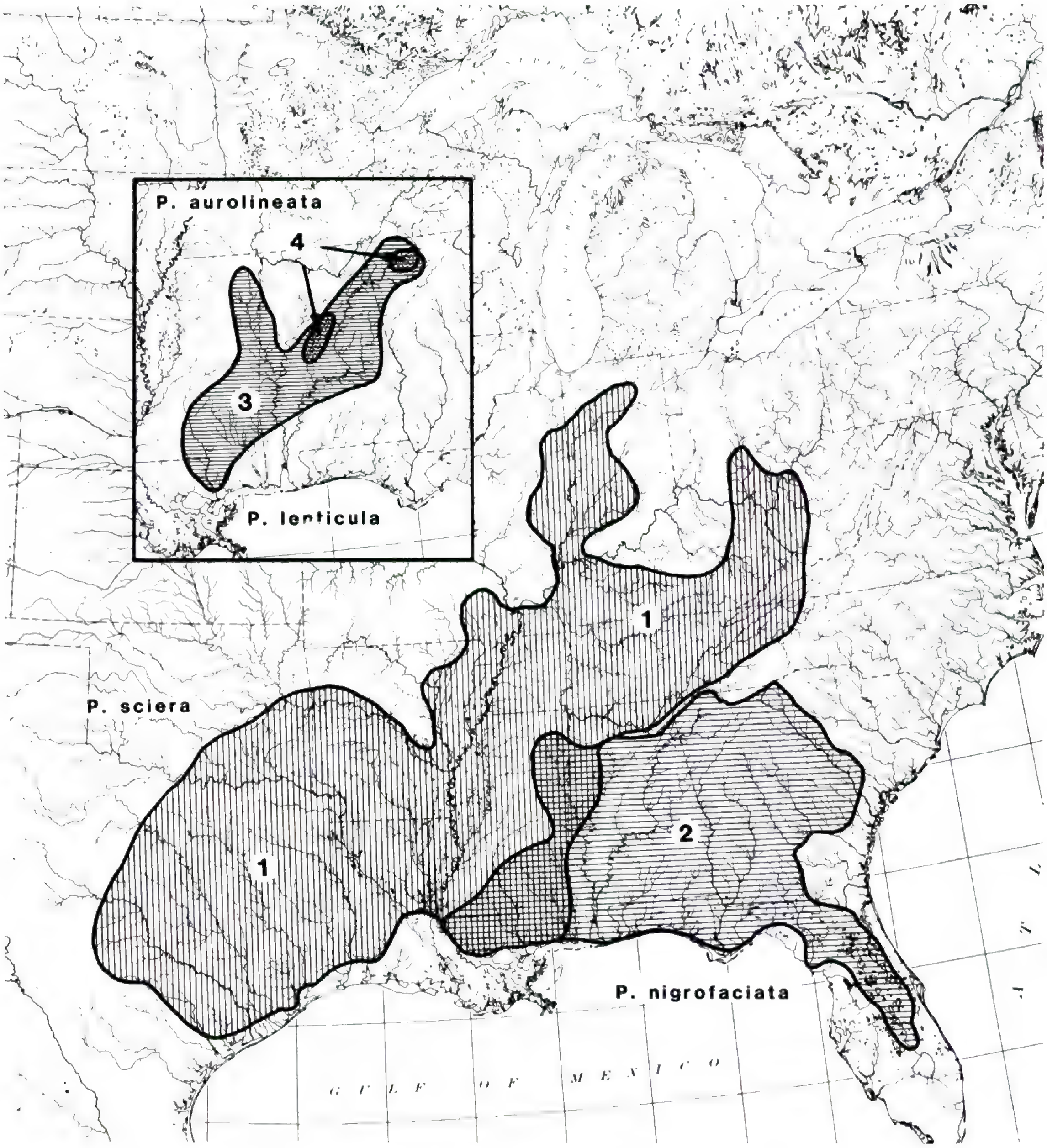

FIGURE 17. Distribution of the subgenus *Hadropterus*, genus *Percina* (from Page, 1974, 1983). Tree: 3+[4+(1+2)]. Characters supporting tree: see Page (1974).

Clades which have one or more of these attributes are listed below. The first five show attributes 1 and 2.

1. *Fundulus catenatus* species group (Fig. 32). *Fundulus catenatus* is found in both highland regions. *Fundulus stellifer* is probably its closest relative (Wiley, in press; data from Williams & Etnier, 1982), and the pair shows a highlands–Mobile Bay pattern similar to *Notropis leuciodes* and *N. chrosomus* (see below). *Fundulus catenatus* in the Interior Highlands comprises two populations, one in the Ozarks, another in the Ouachita Highlands. These highlands were once continuous but were dissected by the present Arkansas River *prior* to the Sangamonian, the interglacial just after the Illinoian Glacier (Quinn, 1958). In addition, there is one disjunct population in Indiana (?Illinoian relict) and at least one in Mississippi (age unknown).

2. The *Hybopsis dissimilis* group (Figs. 33, 34).

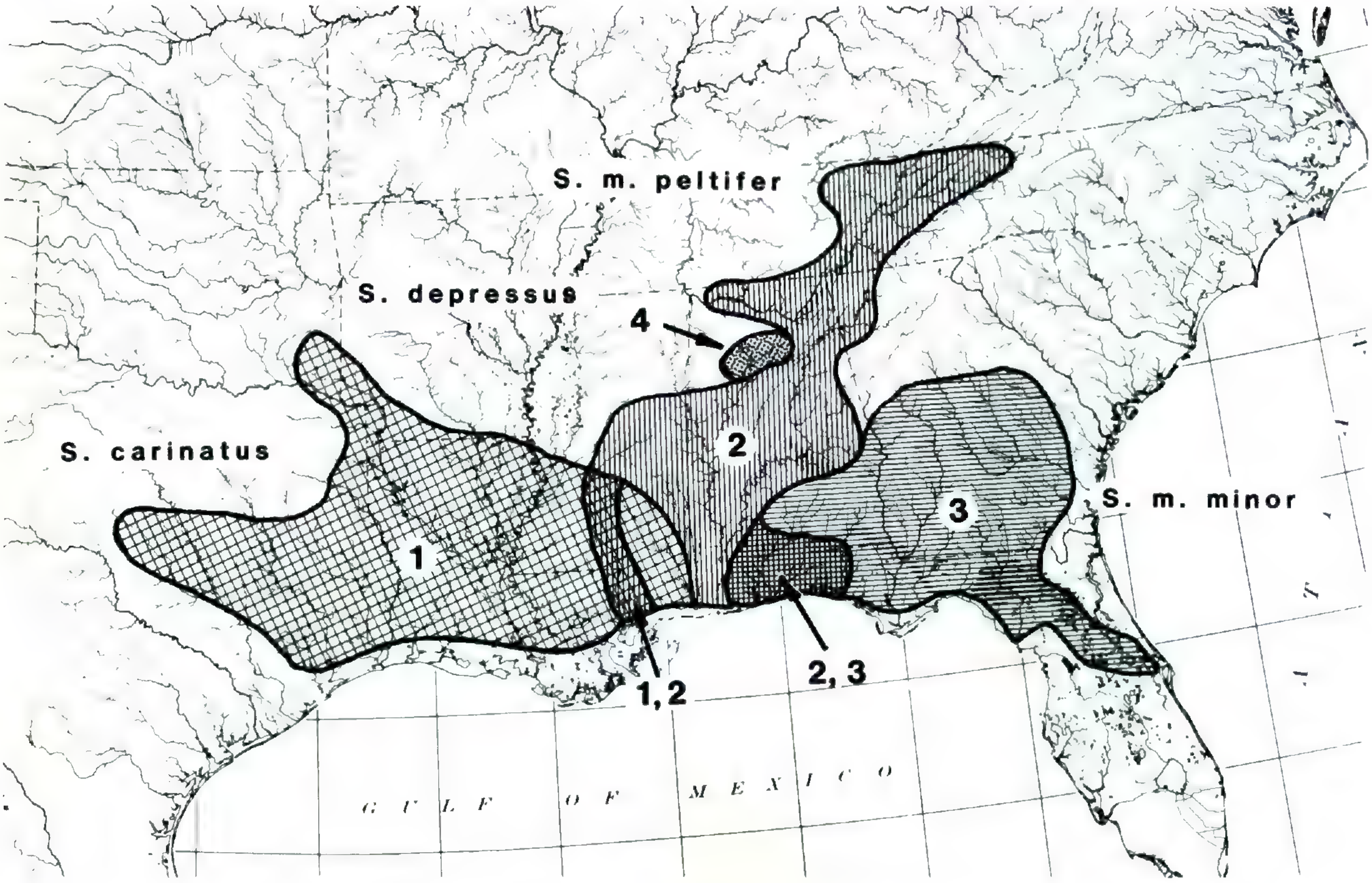

FIGURE 18. Distribution of three species of *Sternotherus* (from Tinkle, 1958). Tree: unresolved.

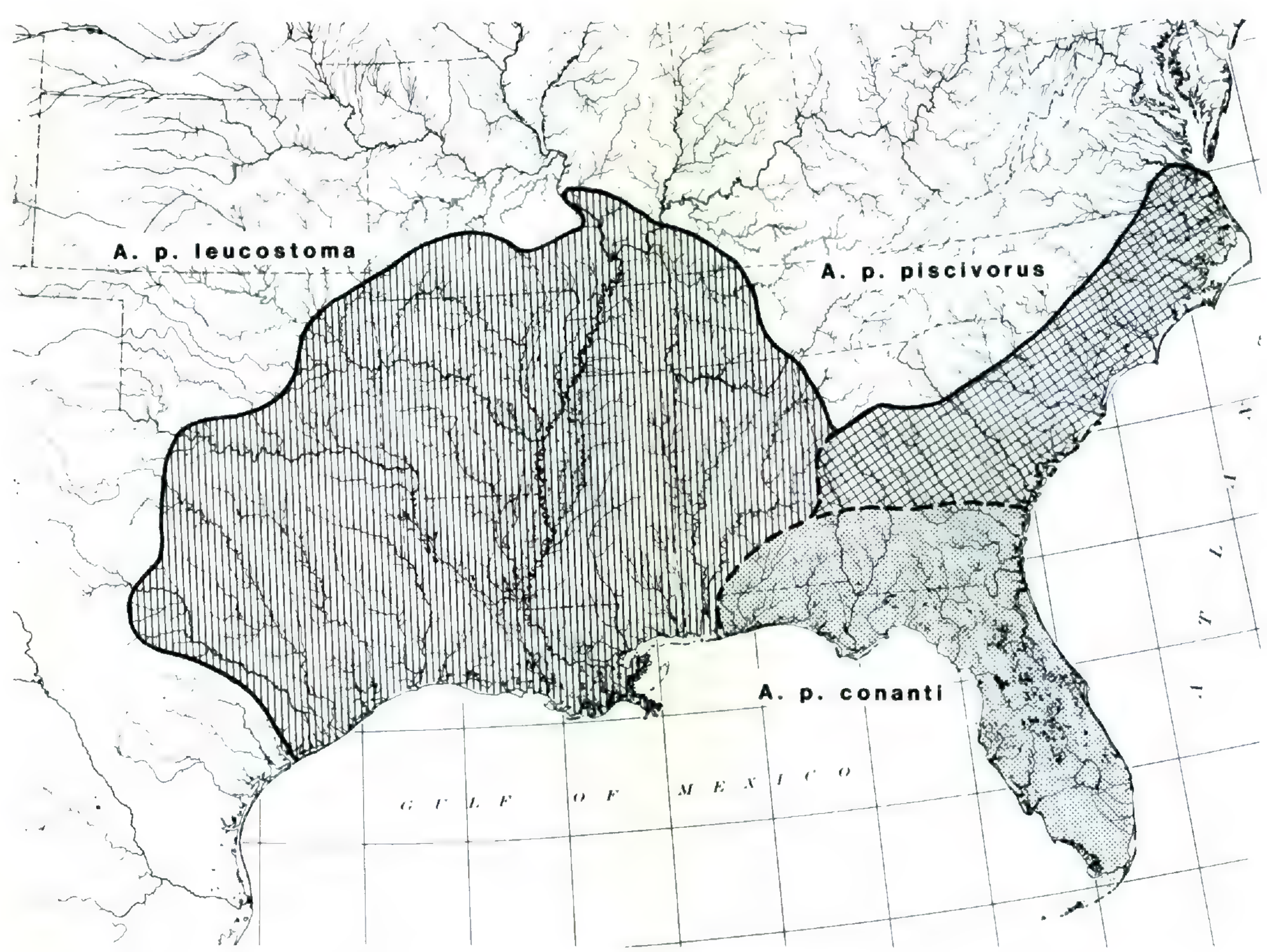

FIGURE 19. Distribution of two subspecies of *Agkistrodon piscivorus* (from Conant, 1975).

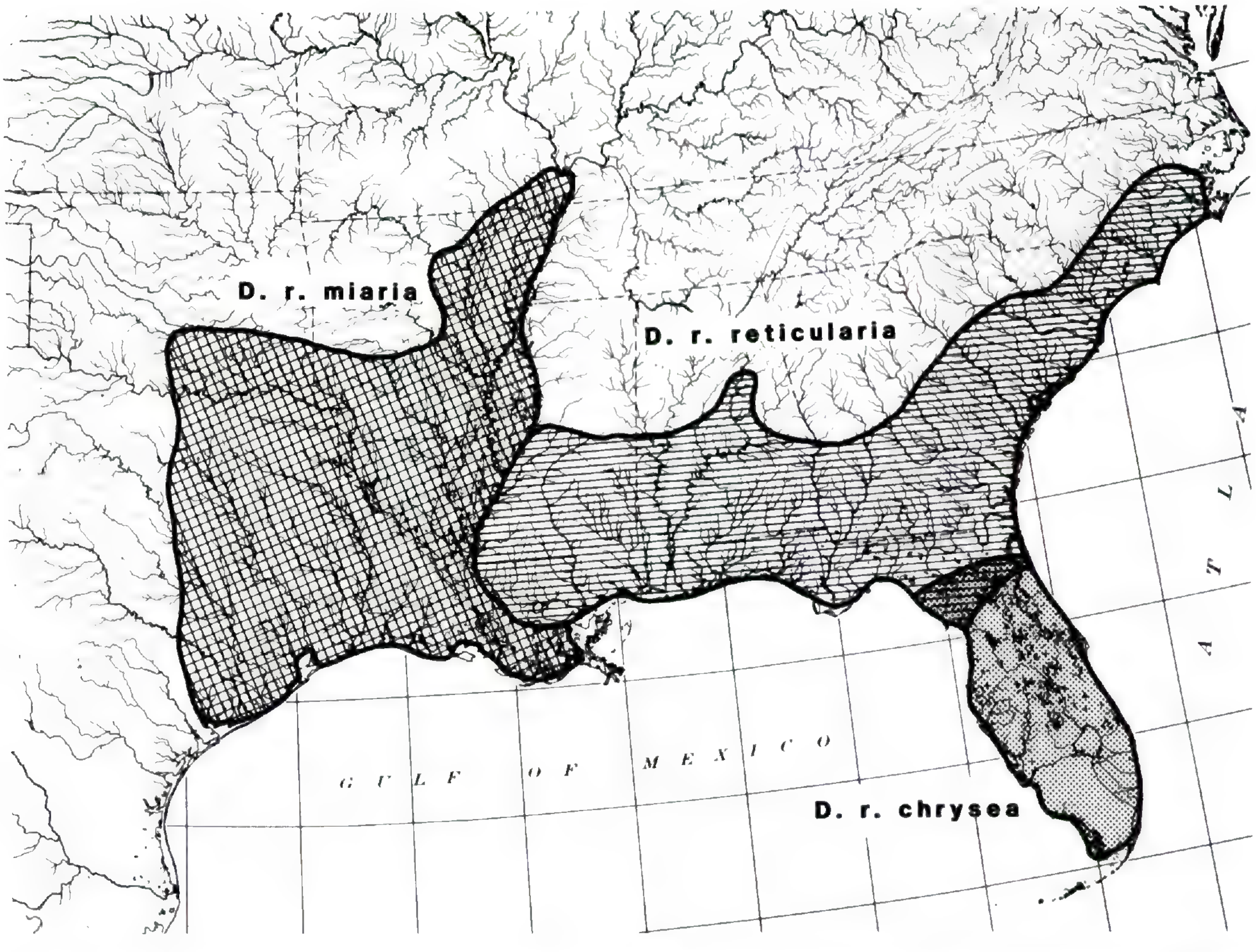

FIGURE 20. Distribution of three subspecies of *Deirochelys reticularia* (from Zug & Schwartz, 1971). Tree: unresolved.

This group contains five species of chubs characterized by having a unique barbel morphology (Mayden, unpubl. data). The species relationships are unanalyzed, but *H. insignis* and *H. dissimilis* share one derived character (presence of lateral pigment blotches on the flanks), which indicates they are sister species. *Hybopsis dissimilis* is found in both highland regions and is broadly sympatric with *H. insignis*. Further, *H. insignis* has a number of relict populations, some of which correspond to regions along the southern edge of the Illinoian Glacier. *Hybopsis x-punctata* is found in the Ozark Highlands and has several disjunct populations including one in the Ouachita Highlands, several north of the Ozarks and several congruent with the eastern disjunct populations of *H. dissimilis*.

3. The *Notropis telescopus* group (Fig. 35). This is a clade of four species, which includes two Eastern Highlands species (*N. semperasper* and *N. scepticus*) as well as two Central Highlands species (*N. telescopus* and *N. ariommus*) (Coburn, 1982). *Notropis telescopus* is found in both highland regions. *Notropis ariommus* is more closely related to the two Eastern Highland species and it has a number of disjunct populations in the Central Lowlands.

4. The *Notropis zonatus–coccogenis* group (Fig. 36). In this case we have five species and two clades (Buth, 1979; Buth & Mayden, 1981; Mayden, unpubl. data). The clades show the Interior-Tennessee split. However, only *N. coccogenis* is a Tennessee form and it is most closely related to *N. zonistius* from the Apalachicola River drainage. Further, *N. pilsbryi* is composed of three disjunct populations, one of which is confined to the Ouachita, dating it as pre-Saga-monian. Thus the origin of *N. zonatus* and *N. pilsbryi* must have occurred prior to this (unless *N. pilsbryi* is the ancestor of *N. zonatus*).

5. The *Notropis nubilus* group (Fig. 37). Three species are members of this clade (Swift, 1970). Two are found in the highlands and one in the Mobile Bay drainage. Relationships among the three are unresolved. If two highland species, *N. nubilus* and *N. leuciodus*, are closest relatives,

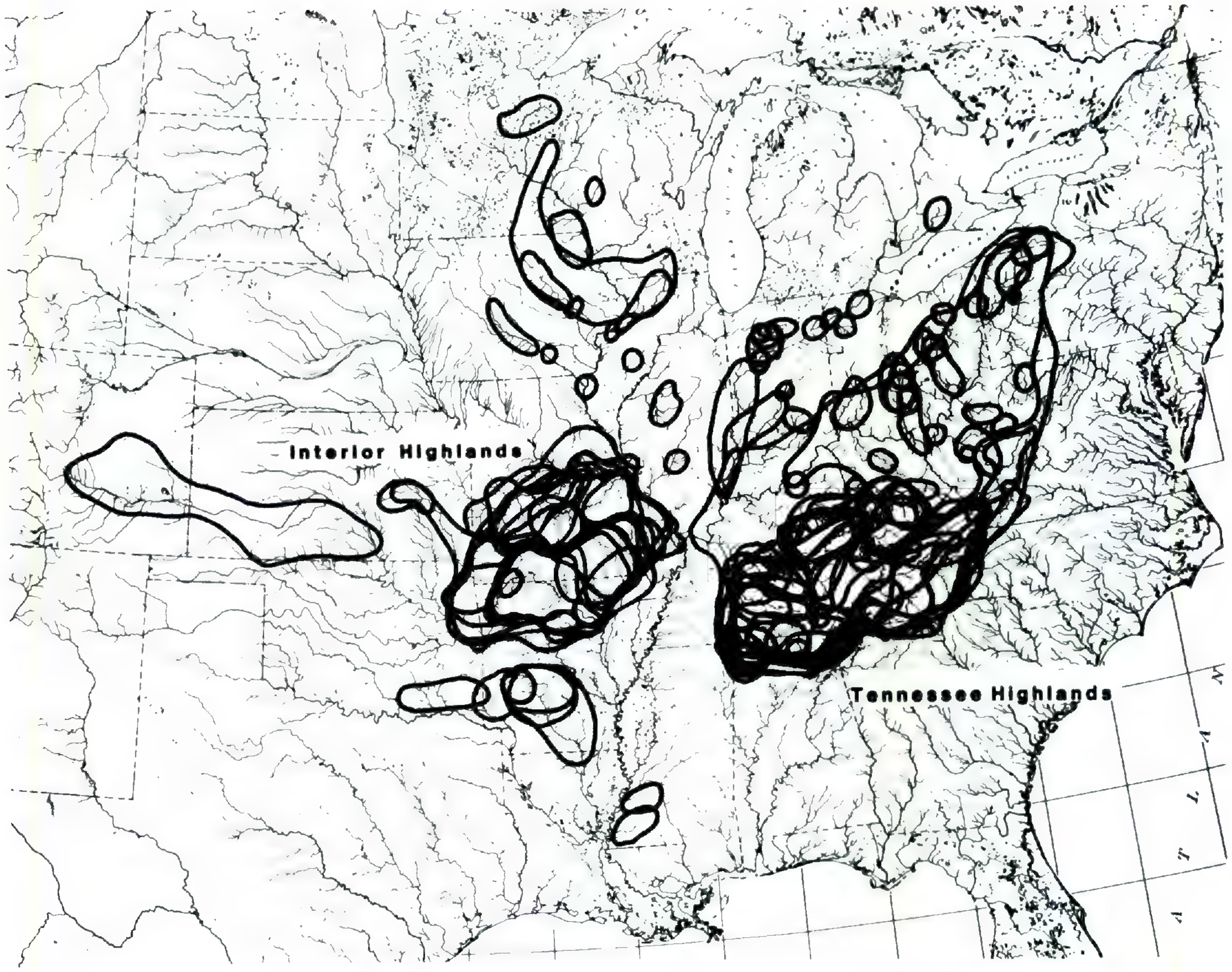

FIGURE 21. Composite ranges of 44 species of fishes largely confined to the Central Highlands of the United States, including disjunct populations found outside the region (mostly from Lee et al., 1980).

then the group would seem to be a candidate for the Pleistocene hypothesis. However, *N. nubilus* has a northern disjunct population that occurs, in part, in the "Driftless Area" of Wisconsin, Minnesota, and Iowa (Flint, 1957) and is probably a pre-Pleistocene relict (Pflieger, 1971). In addition, *N. nubilus* has a coiled gut found only in one other unrelated member of the genus (Swift, 1970; Snelson, 1971) indicating that it cannot be considered an ancestor that dispersed eastward during the Pleistocene to give rise to the eastern members of the clade.

6. The *Etheostoma variatum* group (Fig. 38). This group of darters comprises six species (Hubbs & Black, 1940; Richards, 1966; Mayden, unpubl. data). It is interesting because the Inte-

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FIGURE 22. Pre-Pleistocene drainage patterns of the Central Highlands and adjacent regions. 1 = Plains Stream, 2 = Red River, 3 = Ouachita River, 4 = Arkansas River, 5 = White River, 6 = Grand River, 7 = Iowa River, 8 = upper Mississippi River, 9 = Teays River, 10 = Cumberland and Tennessee Rivers. (Modified from Mayden, 1985.)

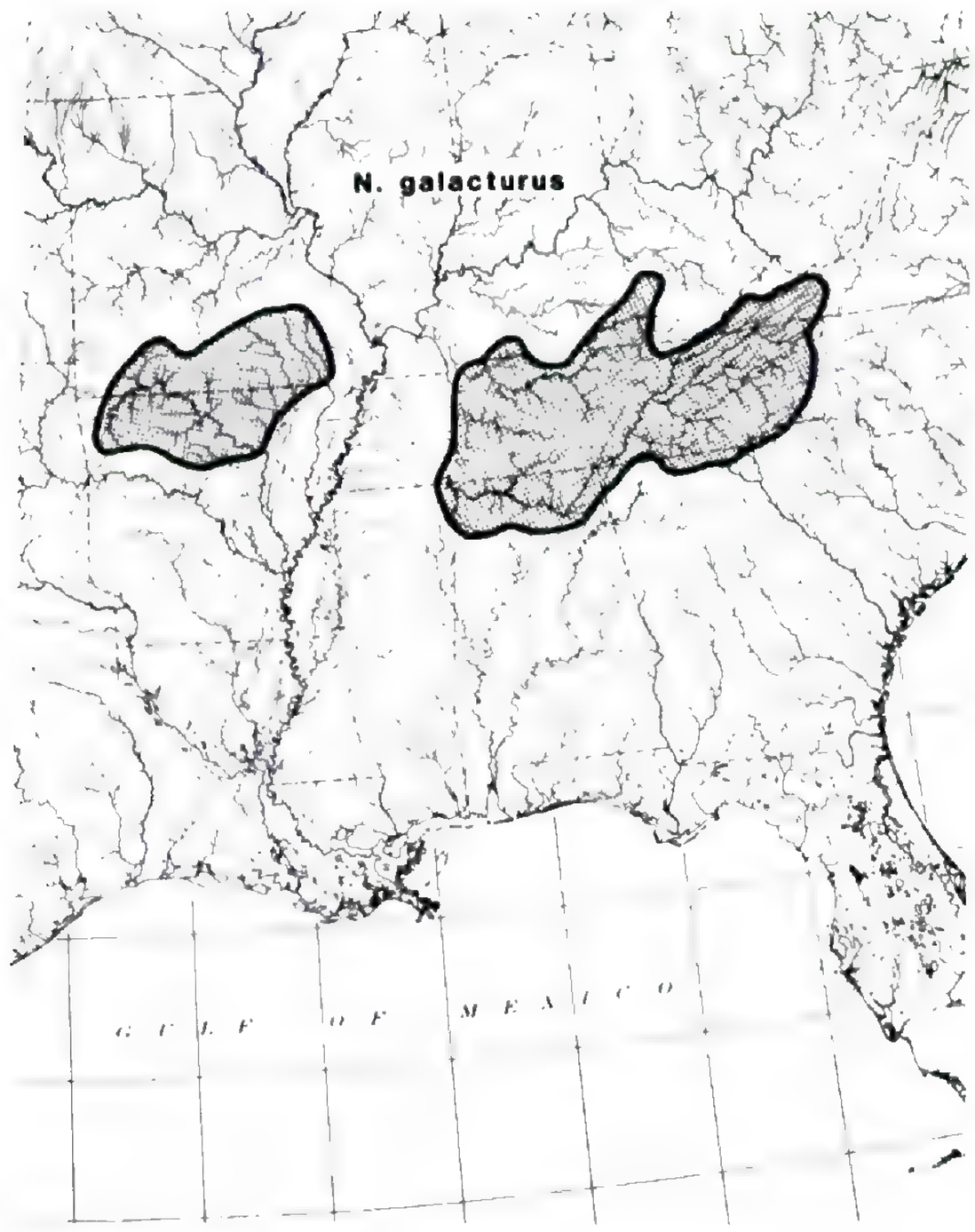

FIGURE 23. Distribution of *Notropis galacturus* (from Lee et al., 1980).

rior-Tennessee split does not correspond to two monophyletic groups. Rather, *E. blennius* is the oldest member of the group and there is evidence that there was a separation of the southern part of the Tennessee Highlands from the presumably continuous highland fauna to the north and west (essentially Tennessee River versus Teays-Mississippi). The next speciation event involved *E. sellare* and the ancestor of the remaining species and was a highlands versus East Coast vicariance event whose basis we cannot interpret (stream capture/peripheral isolation?). The remaining four species form a clade and have an Interior-Tennessee distribution. Whether the speciation event that separated members of this clade was the result of Pleistocene glaciation is problematical. However, we could resolve this by showing that the origin of the *E. osburni–E. kanawhae* species pair was early Pleistocene or pre-Pleistocene. Unfortunately there are no data concerning the age of the Kanawha Falls (Hocutt et al., 1978), the geological feature that marks the boundary between these species and their sister, *E. variatum*. Alternately we could test the hypothesis by dating the time of origin of *E. tetrazonum* and *E. euzonum*. Thus this clade may show "attribute 3" patterns, but this hypothesis awaits more data.

Other taxa are of interest. Five additional groups, one species of amphibian and four fish groups, deserve mention as possible examples pertinent to our analysis.

1. *Cryptobranchus alleganiensis* has an overall distribution similar to the *Etheostoma variatum* group. One subspecies *alleganiensis* is found in both highland regions and there is a disjunct population on the East Coast (Fig. 39).

The four fish groups comprise either a single species for which subspecies are recognized or several closely related species. Lack of phylogenetic hypotheses concerning their relationships precludes their use in the analysis.

2. The subgenus *Swainia*, genus *Percina* (Fig. 40). The group contains four highland darters (one undescribed) and a widespread species (*P. phoxocephala*) not confined to highland habitats (Page, 1974).

3. The *Etheostoma maculatum* species group (Fig. 41). This group is interesting in having highland species, disjunct populations of one species (*E. maculatum*), and a southern disjunct species found in the drainage adjacent to that containing the southern disjunct population of *Fundulus catenatus* (Williams & Etnier, 1982). Thus it contains species relevent to testing a Gulf Coastal Plain connection as well as a highlands connection.

4. *Etheostoma blennioides*. Several subspecies are recognized (Miller, 1968), and the distribution of these is similar to others included in the analysis.

5. *Cottus carolinae*. This species includes three highland subspecies and a subspecies endemic to the eastern Mobile Bay drainage (Lee et al., 1980).

Vicariance—the Central Highlands—discussion. The evidence we have presented indicates that speciation in highland fishes cannot be correlated with the vicariance of the Central Highlands by the Illinoian Glacier. Rather, the evidence indicates that most or all of the species analyzed were present and living in the region before the Pleistocene and thus speciated over a landscape including drainage patterns not found today. Our data are not consistent with the idea that most of the groups analyzed lived north of their present distribution and were pushed south by glaciers to inhabit their present ranges, because several clades have relatives in the Coastal Plain (Mobile and Apalachicola drainages) and some have relatives on the Atlantic slope. This implies a history of contact between the high-

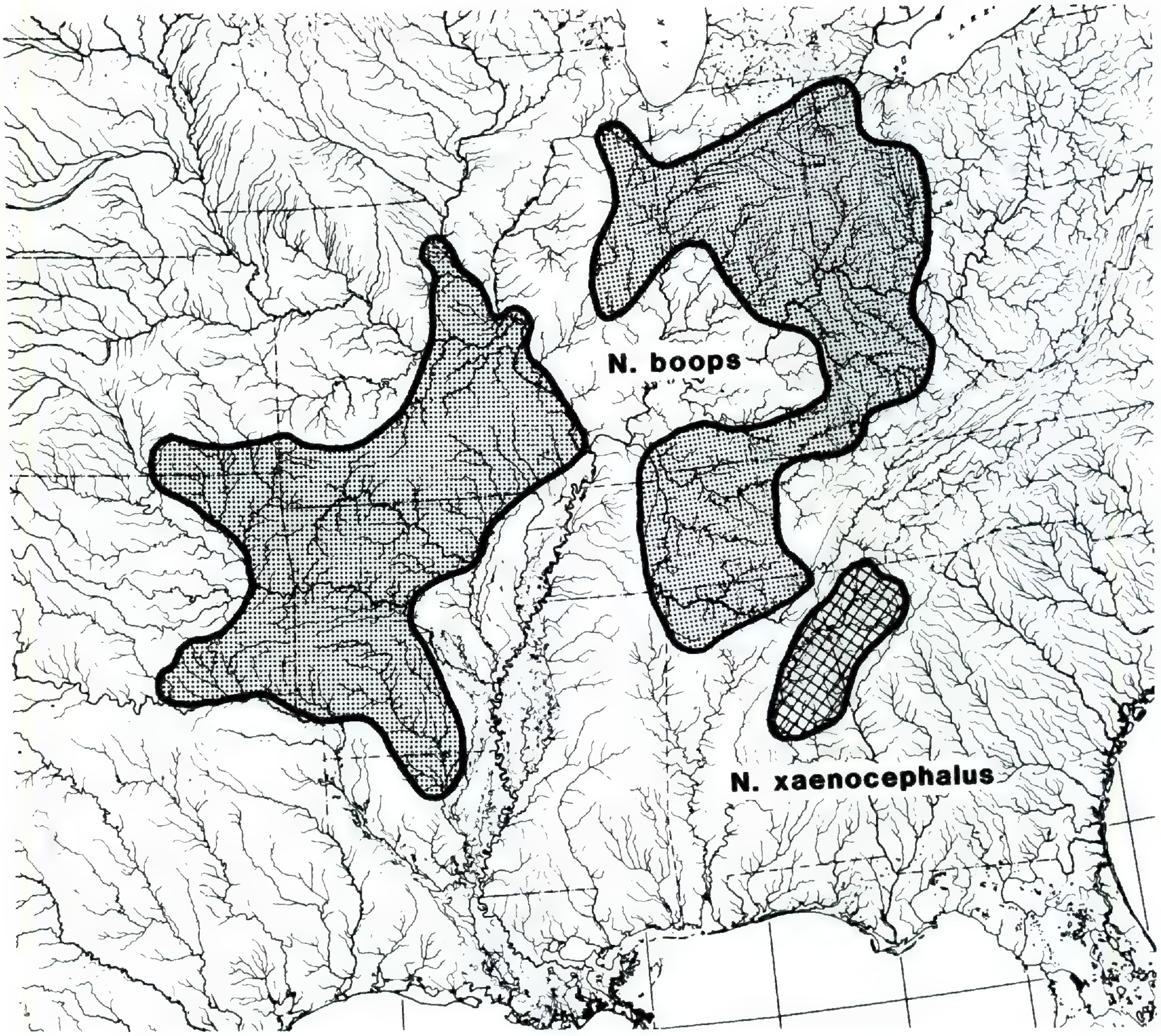

FIGURE 24. Distribution of *Notropis boops* and *N. xaenocephalus* (from Burr & Dimmick, 1983).

lands and the Gulf Coastal Plain. We *do not* wish to imply that the present disjunction is not correlated with the Illinoian Glacier. It probably did cause the disjunction we now observe by modifying the area north of the present highlands into the Central Lowlands. Further, we *do not* wish to imply that some speciation within either the Interior Highlands or the Tennessee Highlands had no correlation with Pleistocene events. It probably did. What we do wish to imply is that the simplest explanation for speciation observed in three species pairs we first discussed is not corroborated when we analyze the fauna as a whole. While large-scale vicariance speciation (Model I) might explain much of the evolution in the clades we have analyzed, glaciation does not provide a simple causal mechanism of vicariance correlated with speciation.

ALLOPATRIC SPECIATION II—PERIPHERAL ISOLATION

Peripheral isolation models postulate the origin of a new species in a very small portion of the range of an ancestor or colonization and subsequent differentiation of a part of the earth not occupied by the ancestor. One problem with deducing phylogenetic and biogeographic predictions from this mode is that there are at least two different processes that may be involved. In the case of what might be called "classic" peripheral isolation, the model invoked has a distinct ecological component as well as a historical component. New species arise in marginal habitats, usually but not always at the periphery of the ancestral range. This is the model favored by Mayr (1963), Hennig (1966), and Brundin (1966).

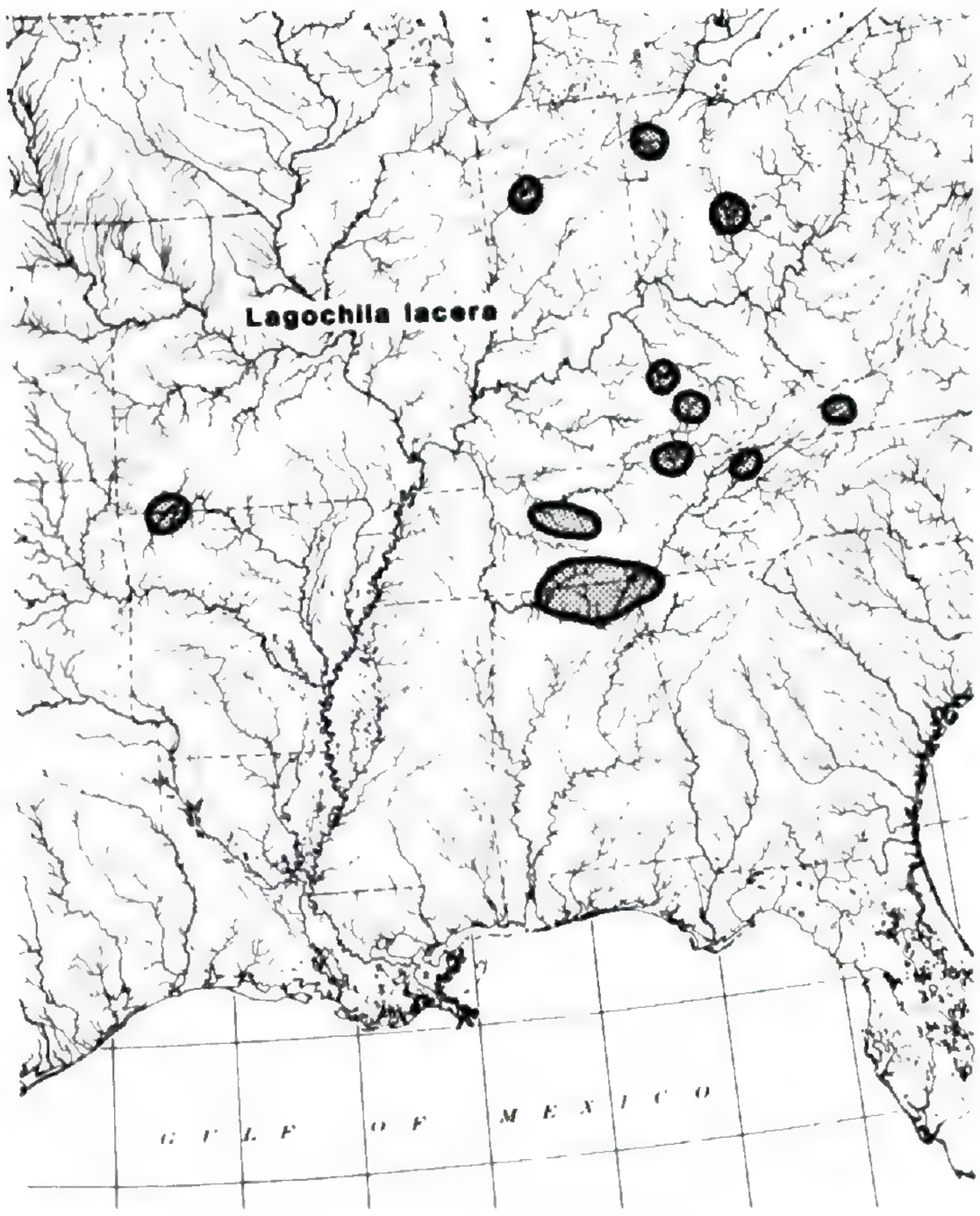

FIGURE 25. Known collection localities of *Lagochila lacera* (now extinct, from Lee et al., 1980).

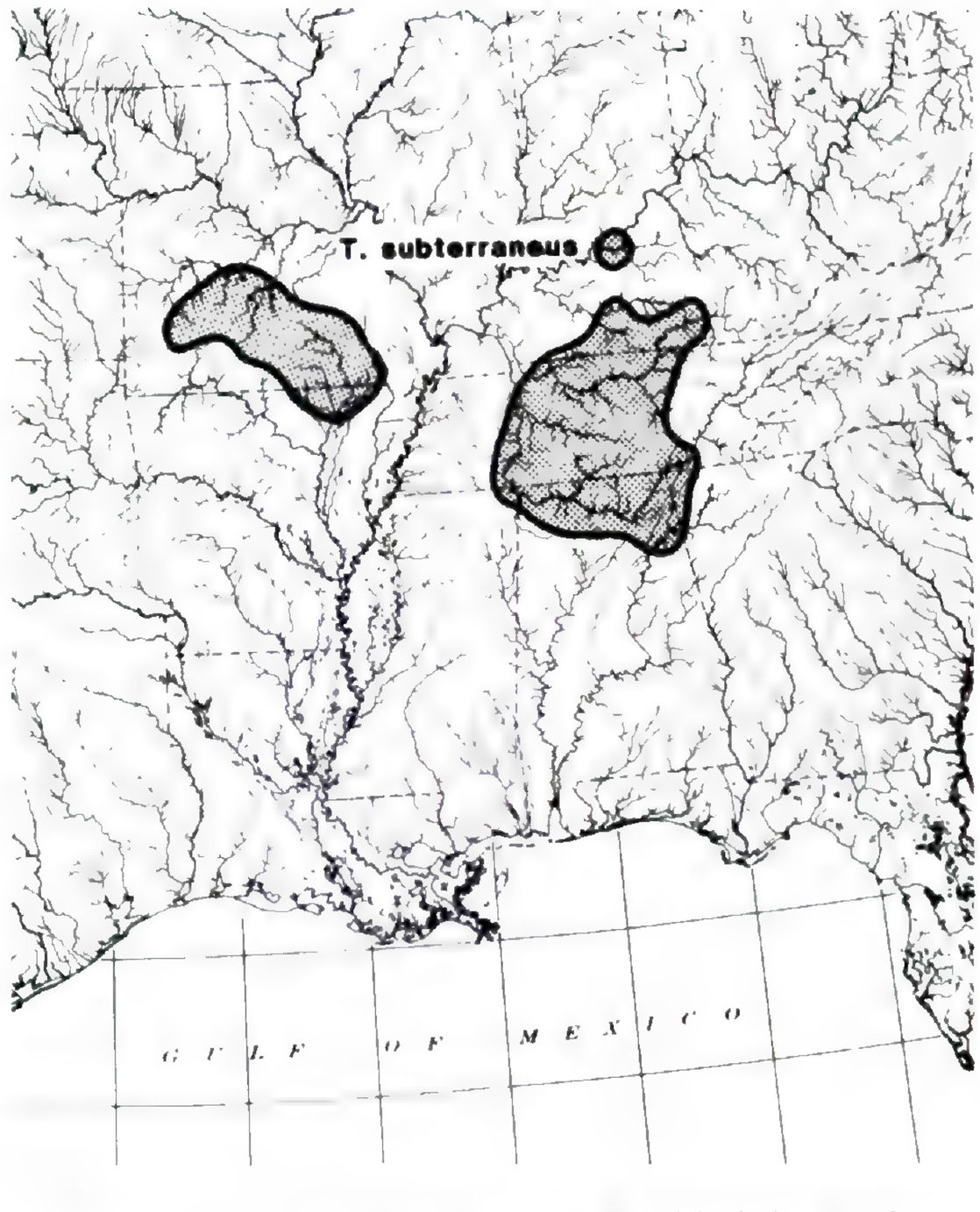

FIGURE 26. Distribution of *Typhlichthys subterraneus* (from Lee et al., 1980).

It includes the notion that populations inhabiting marginal areas are somewhat free to diverge from the central population because of decreased gene flow. At least some, including Hennig (1966), also assert that differentiation occurs in response to the different ecological conditions encountered by the isolated population.

In "vicariant" peripheral isolation, the model invoked has a historical component but not necessarily an ecological component. It is simply the end of a continuum of possibilities for subdividing an ancestral species, with large-scale vicariance involving large chunks of range and peripheral isolates involving very small chunks.

The commonality shared by these two types of peripheral isolation concern the characteristics of the ancestor relative to the descendant. Specifically, the ancestor is thought to survive the speciation event unchanged or largely unchanged, whereas the peripheral isolate diverges (cf. Mayr, 1963; Grant, 1971; Eldredge & Gould, 1972). Whether or not the ancestor "really survives" is not the issue, rather, the issue is whether the large population evolves to any significant degree in a manner correlated with the speciation event. When we say "really survives" we refer to various metaphysical arguments dating to Hennig's (1966) methodological conclusion that ancestral species always go "extinct" at branch points. We do not believe it is necessary to postulate this. Without arguing the merits of the metaphysical case (we have no stake in the outcome of such an argument), the hypothesis is clear. Hennig's (1966) deviation rule applies. One species, the peripheral isolate, diverges more from the ancestral condition than the other. A variety of predictions can be generated under this model (or models). These fall into two general classes, predictions from single speciation events and predictions from multiple speciation events.

Peripheral isolation—single speciation events. Peripheral isolation involving one central population and one peripheral population results in a dichotomous tree at the level of species. Thus the tree pattern is identical to that produced by large-scale vicariance. The biogeography, however, is quite different. We would expect the speciation event to result in a biogeographic topology of a widespread species and a species of very limited range. For example, in the North American killifish genus *Fundulus, F. diaphanus* is a wide-ranging species and its sister species, *F. waccamensis,* is restricted to Lake Waccamaw in North Carolina, and one artificially introduced population (that can be ignored) found in Phelps Lake, North Carolina. In describing *F. waccamensis,* Hubbs and Raney

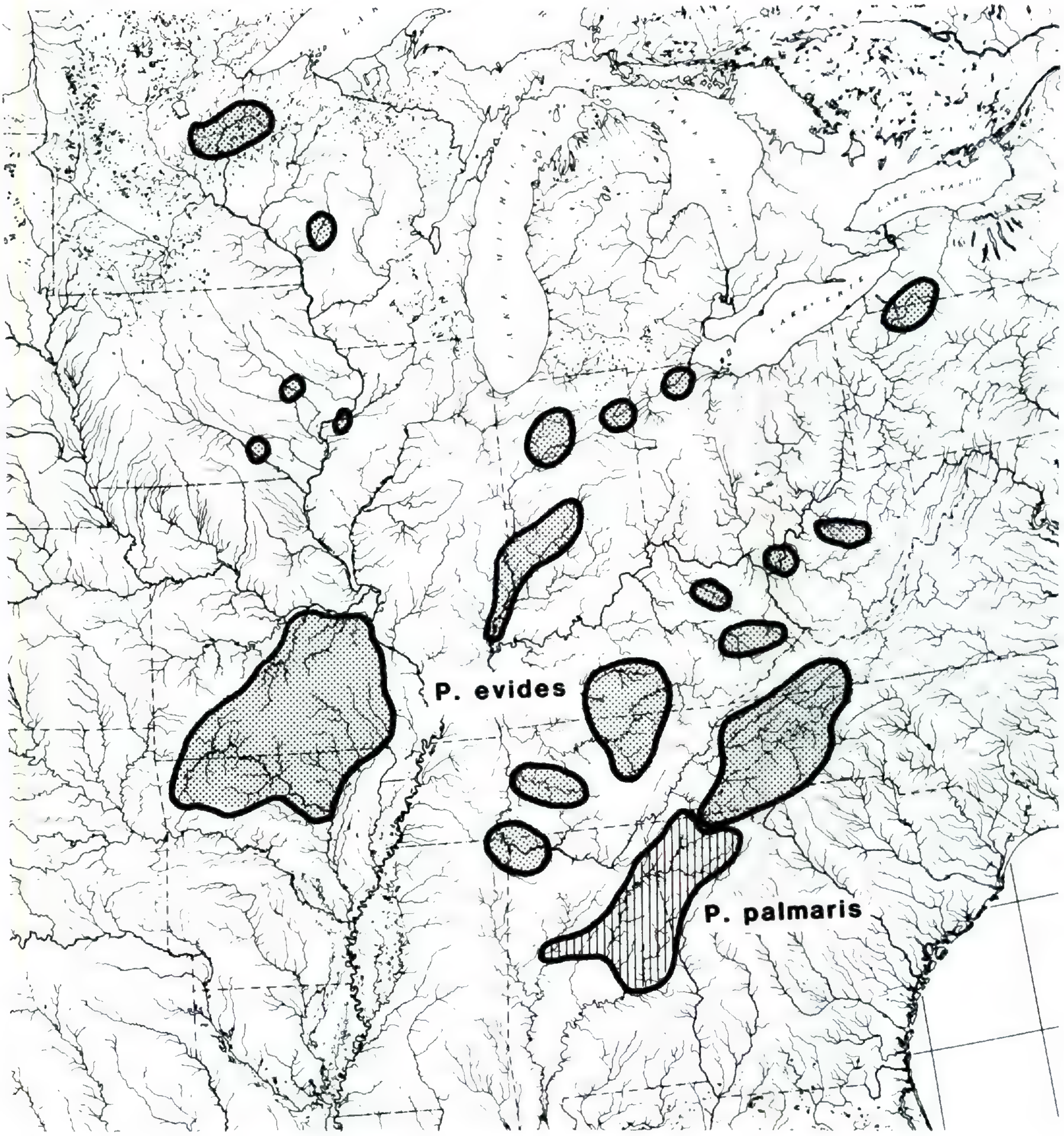

FIGURE 27. Distribution of *Percina evides* and *P. palmaris* (from Page, 1983).

(1946) suggested that it was a peripheral isolate derived from *F. diaphanus*. To what extent is this hypothesis justified?

One problem in considering this hypothesis is that the ranges now occupied by *F. diaphanus* and *F. waccamensis* could have been achieved in several different ways. In Figure 42a we show the geographic relationships between two hypothetical species, A and B. In Figure 42b we show the origin of B as a peripheral isolate derived from a "small-scale" vicariance event. (The same effect would be achieved by dispersal of one or more populations ancestral to B into the area followed by differentiation.) This hypothetical scenario, similar to that favored by Hubbs and Raney (1946), requires little or no alterations in the range of A nor does it require scenarios invoking large-scale populational extinctions. The same result, however, could be achieved by very different scenarios, three of which are shown in Figure 42c, d, and e. These include (1) peripheral isolation of A with subsequent displacement of B into its present range (Fig. 42c), (2) a large-scale vicariance event resulting in the origins of both A and B, with subsequent displacement of B (Fig. 42d), and (3) widespread extinction of the

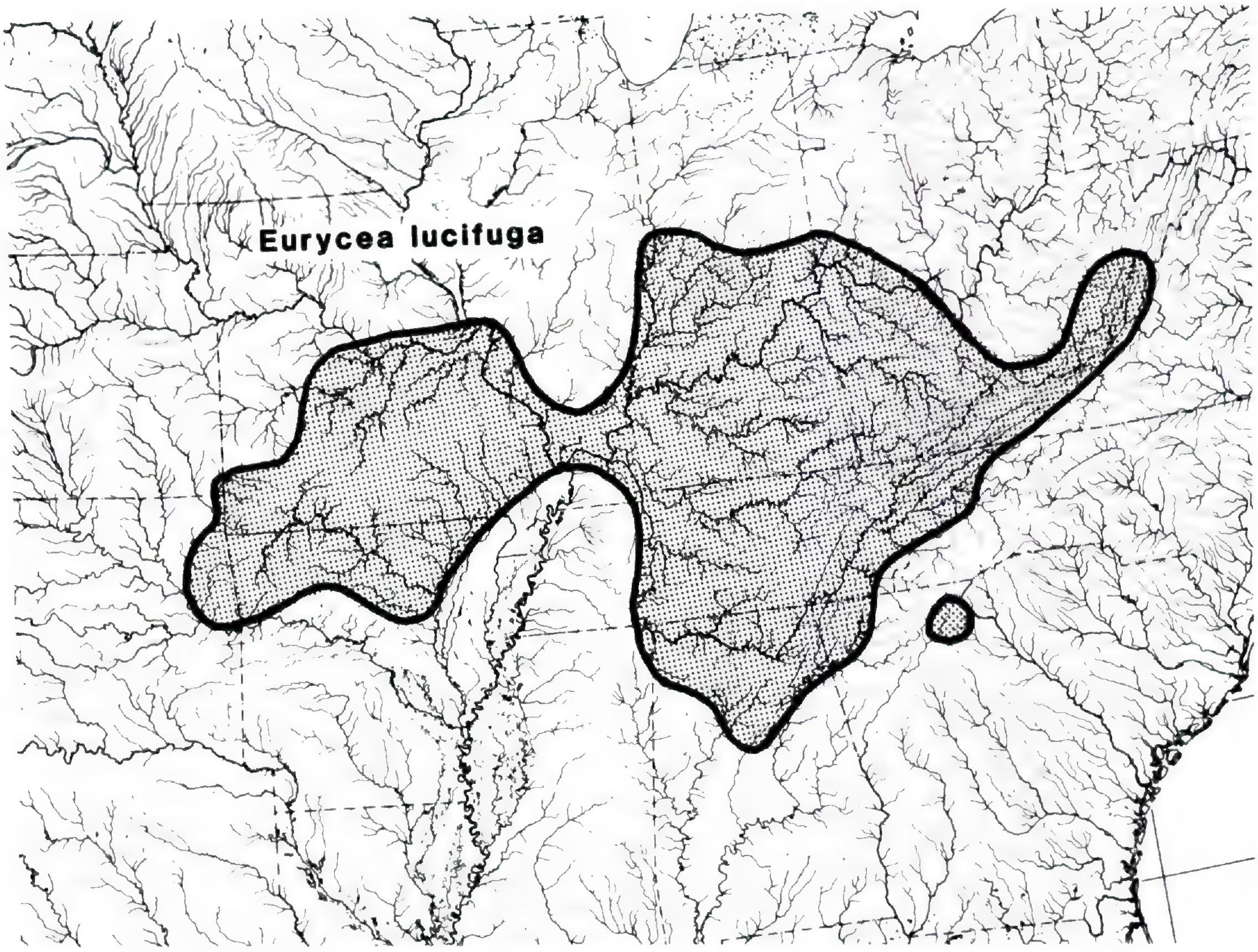

FIGURE 28. Distribution of *Eurycea lucifuga* (from Conant, 1975).

original ancestral populations with both A and B originating in the resulting refugia, followed by a re-invasion of the original range of the ancestor by A (Fig. 42e). The problem is—how can we sort out these four very different scenarios?

One rather direct approach might be to adopt a parsimony argument and claim that it is simpler to adopt a model that requires no extinctions or dispersal (i.e., Fig. 42b) because such a model contains the fewest *ad hoc* assumptions. We would reject this purely logical approach for two reasons. First, parsimony is a logical device and cannot be used to test a proposition. It proceeds by weighing conflicting data and there are none. Second, the importance (or lack thereof) ascribed to this model of speciation by some make it important enough to be approached with some caution.

We suggest that certain lines of evidence might be developed. Some are "extrinsic" in that they deal with data concerning the histories of the respective geographic areas inhabited by the species involved. Some are "intrinsic" in that they deal with data derived from the species themselves.

Extrinsic evidence might take several forms. We might demonstrate that there is no evidence for climatic change or large-scale vicariance events occurring in the region presently inhabited by species A that would have effected it or its ancestor. This would reinforce the idea that neither Figure 42d nor e are applicable. We might find that the region occupied by species B either did not exist or was uninhabitable in the recent past, requiring a hypothesis of dispersal into the area. We might be able to identify a "small-scale" vicariance event with the isolation of the ancestral populations of B.

Intrinsic evidence is more difficult to speculate about, because the kinds of data derived from character analysis may depend on levels of gene flow between populations, the time that has passed since vicariance or dispersal, the history (or lack thereof) of gene flow between the isolate and the central population, and the effect (or lack

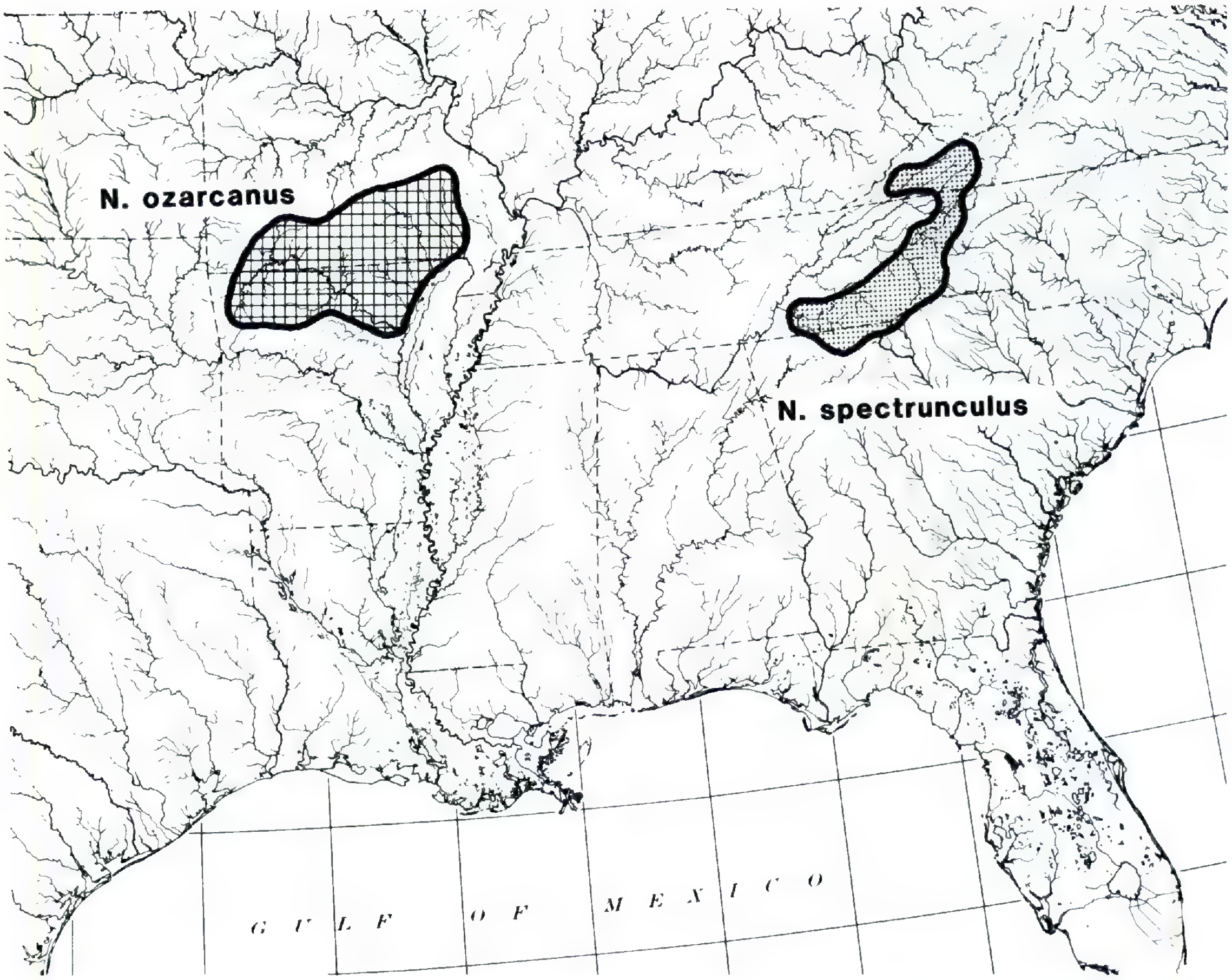

FIGURE 29. Distribution of the *Notropis spectrunculus* species group (from Ramsey, 1965; Mayden, unpubl. data). An undescribed species reported by Branson (1983) is found west of the range of *N. spectrunculus* and it is partly sympatric with this species. We have not plotted the range of the undescribed species for lack of distributional data.

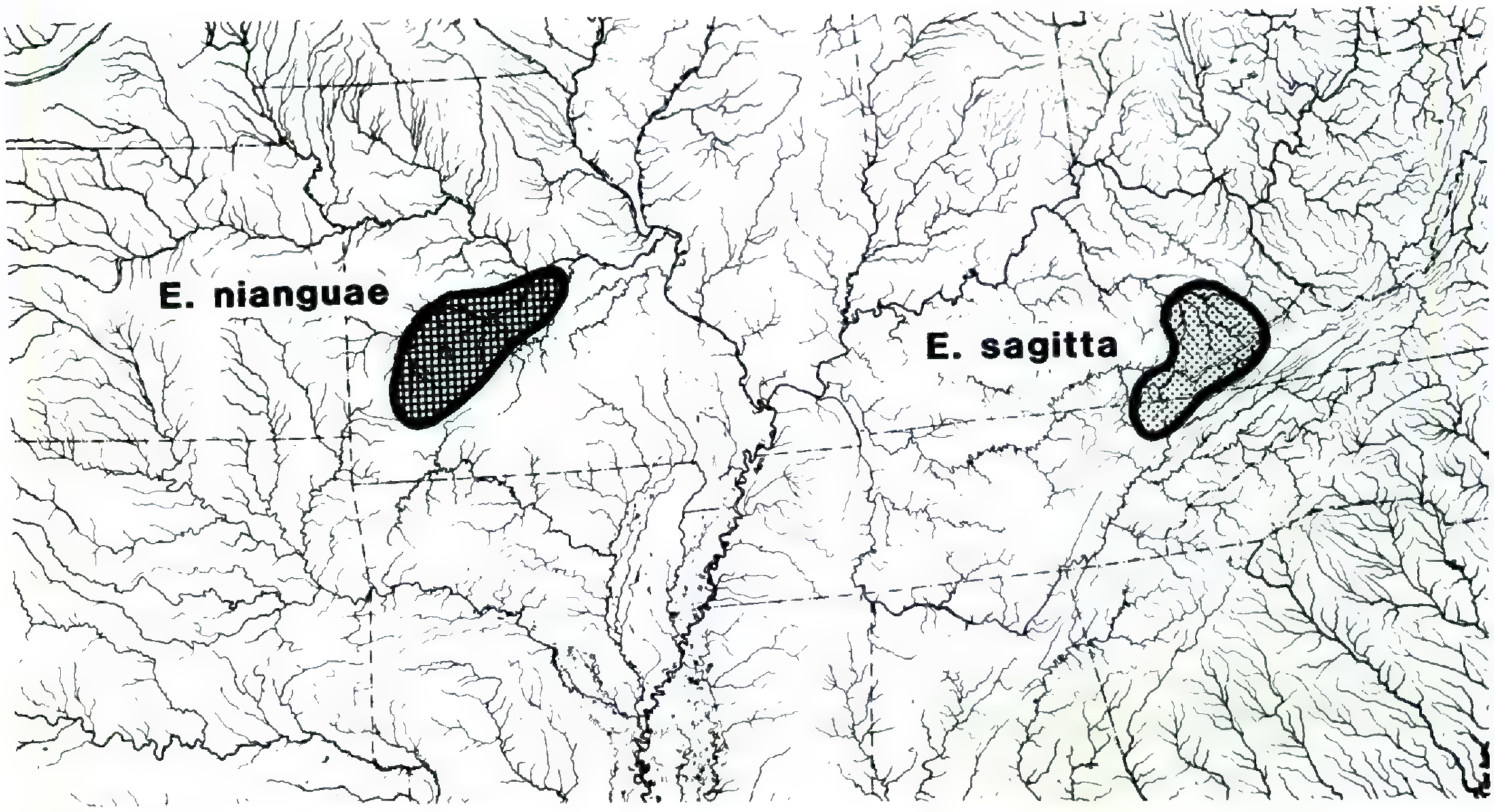

FIGURE 30. Distribution of *Etheostoma niangue* and *E. sagitta* (from Page, 1983).

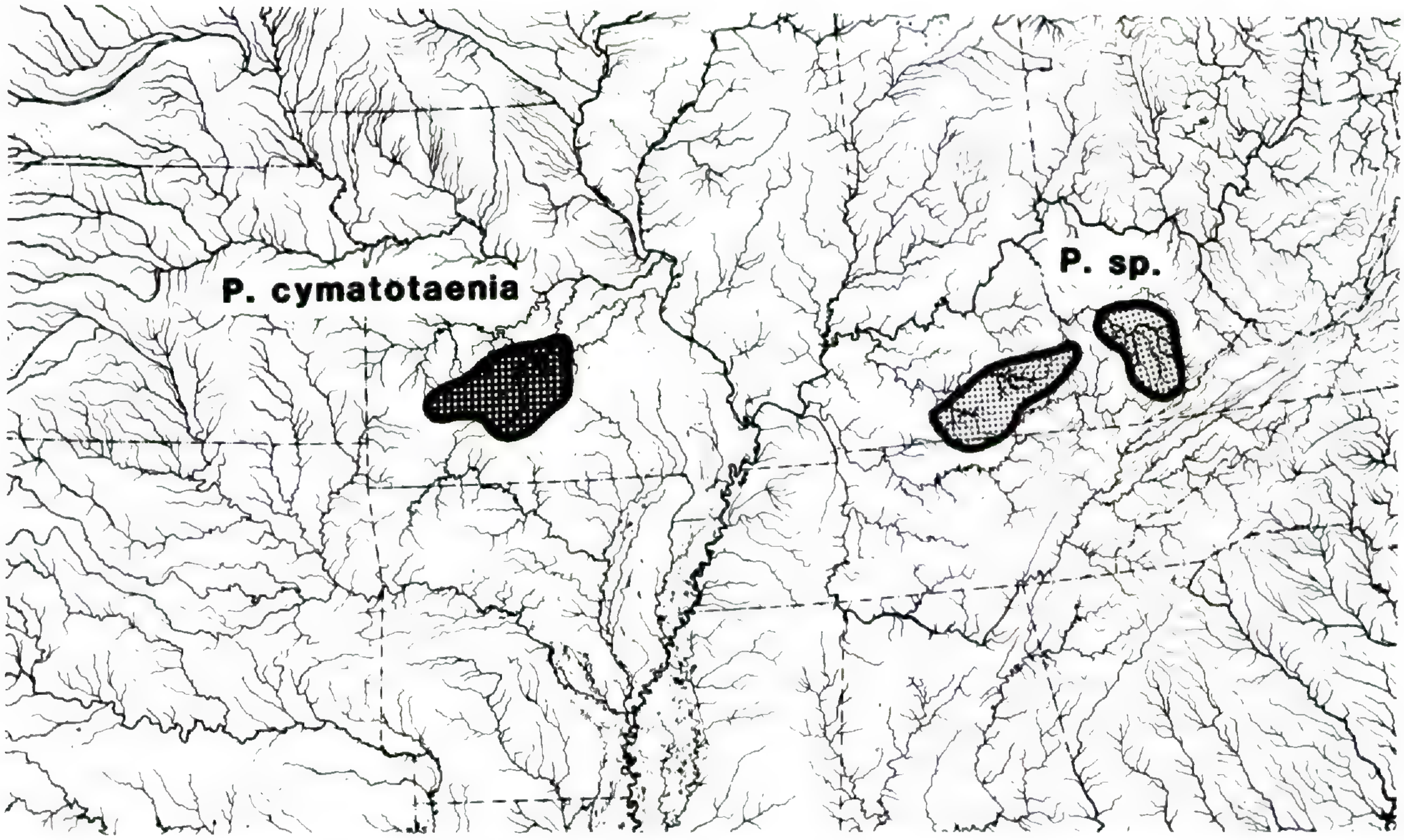

FIGURE 31. Distribution of *Percina cymatotaenia* and an undescribed sister species (from Page, 1983).

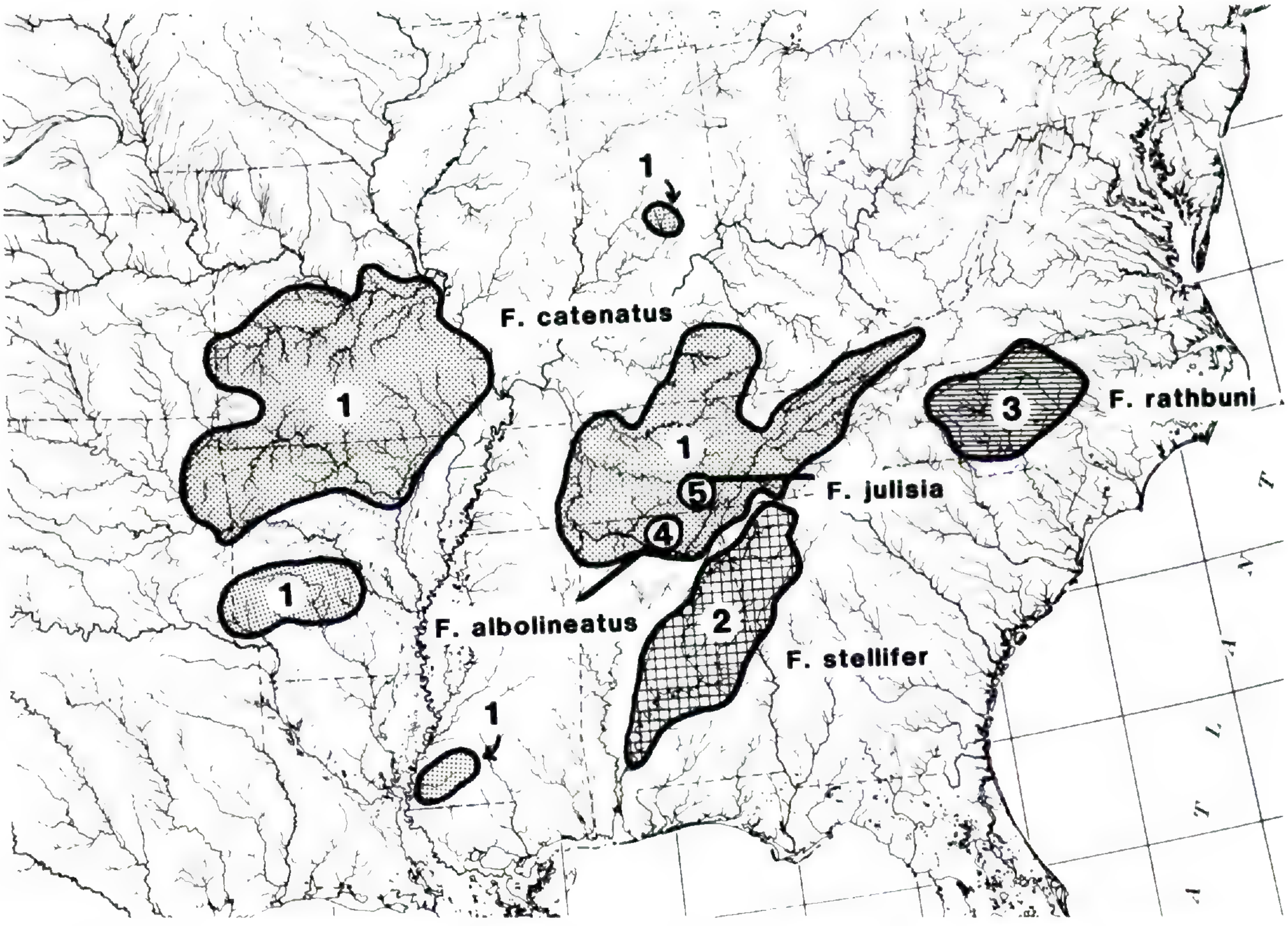

FIGURE 32. Distribution of the *Fundulus catenatus* species group (from Lee et al., 1980 and Williams & Etnier, 1982). Tree: 3+[4+5+(1+2)]. Characters supporting tree: see Wiley (in press).

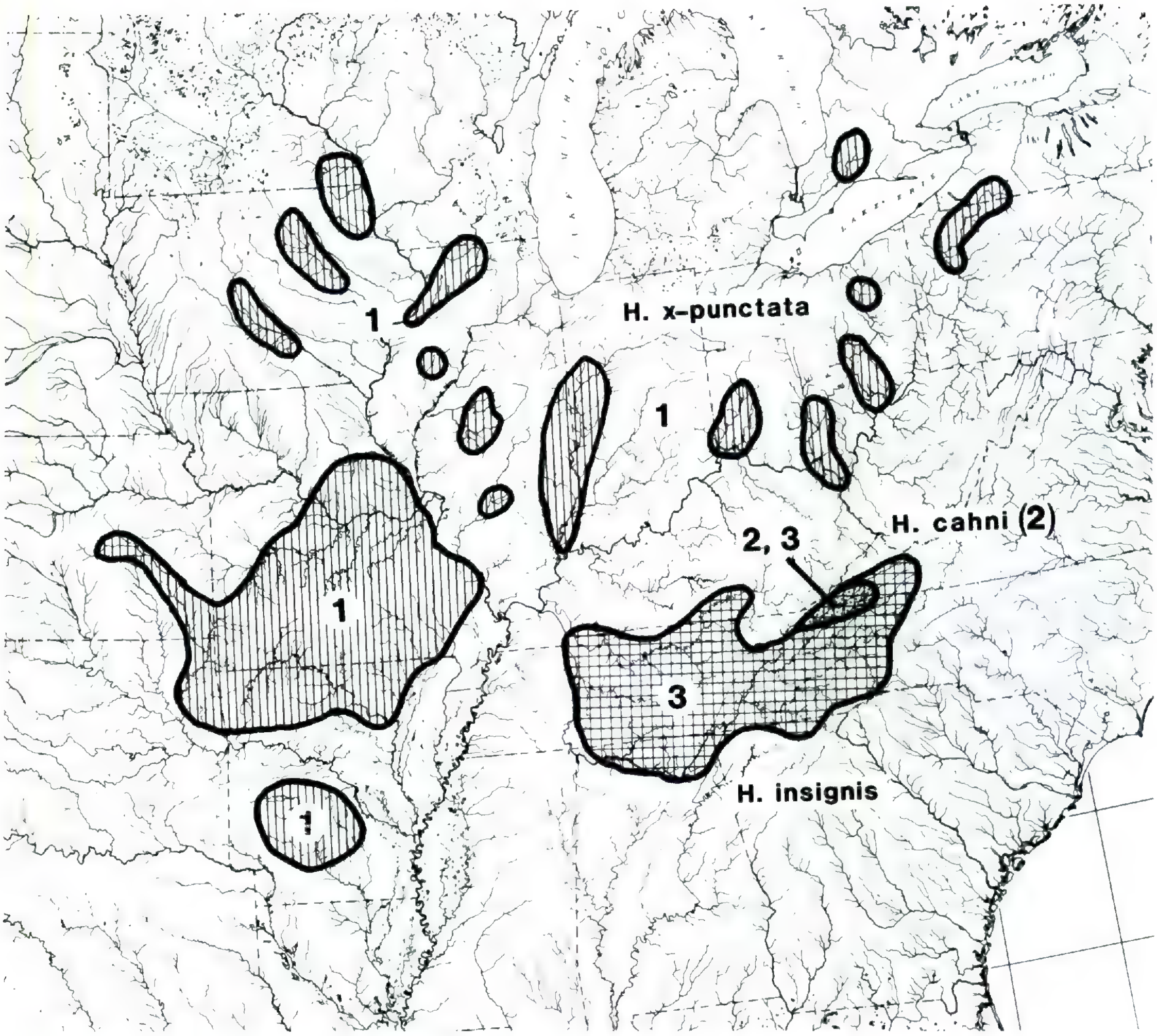

FIGURE 33. Distributions of some of the members of the *Hybopsis dissimilis* species group (from Lee et al., 1980). See Figure 34 for tree and characters supporting the tree.

thereof) of local selection on each population. Controversies exist concerning the population genetical aspects of founder effects and even the importance of peripheral isolation as a mechanism of speciation (for recent contrasting reviews see Carson & Templeton, 1984, and Barton & Charlesworth, 1984). In spite of these problems, we believe that certain lines of inquiry might be fruitful.

One line of inquiry might be developed around the notion that peripheral isolates diverge more than the central population. In a two-species system we might observe more fixed differences in the putative peripheral isolate relative to the reconstructed ancestral phenotype or genotype. For this to count, however, we would have to assume that the characters examined represent a random sample of all characters that have diverged. Further, lack of a sharp deviation (that is, the presence of equal divergence in both lineages) might be compatible with peripheral isolation if the two species are of sufficiently ancient origin (thus providing time for anagenesis in the wide-ranging species) and the wide-ranging species is characterized by high levels of gene flow (thus providing the opportunity for the spread of evolutionary novelties).

Another line of evidence might be developed by considering the geographic variation of certain kinds of characters. If species B is a peripheral isolate, it was probably derived from populations of A near its range or, alternately, was in genetic contact with such populations before vicariance. This is probable if the scenario presented in Figure 4b is true. Rapidly evolving systems, especially if they were immune from se-

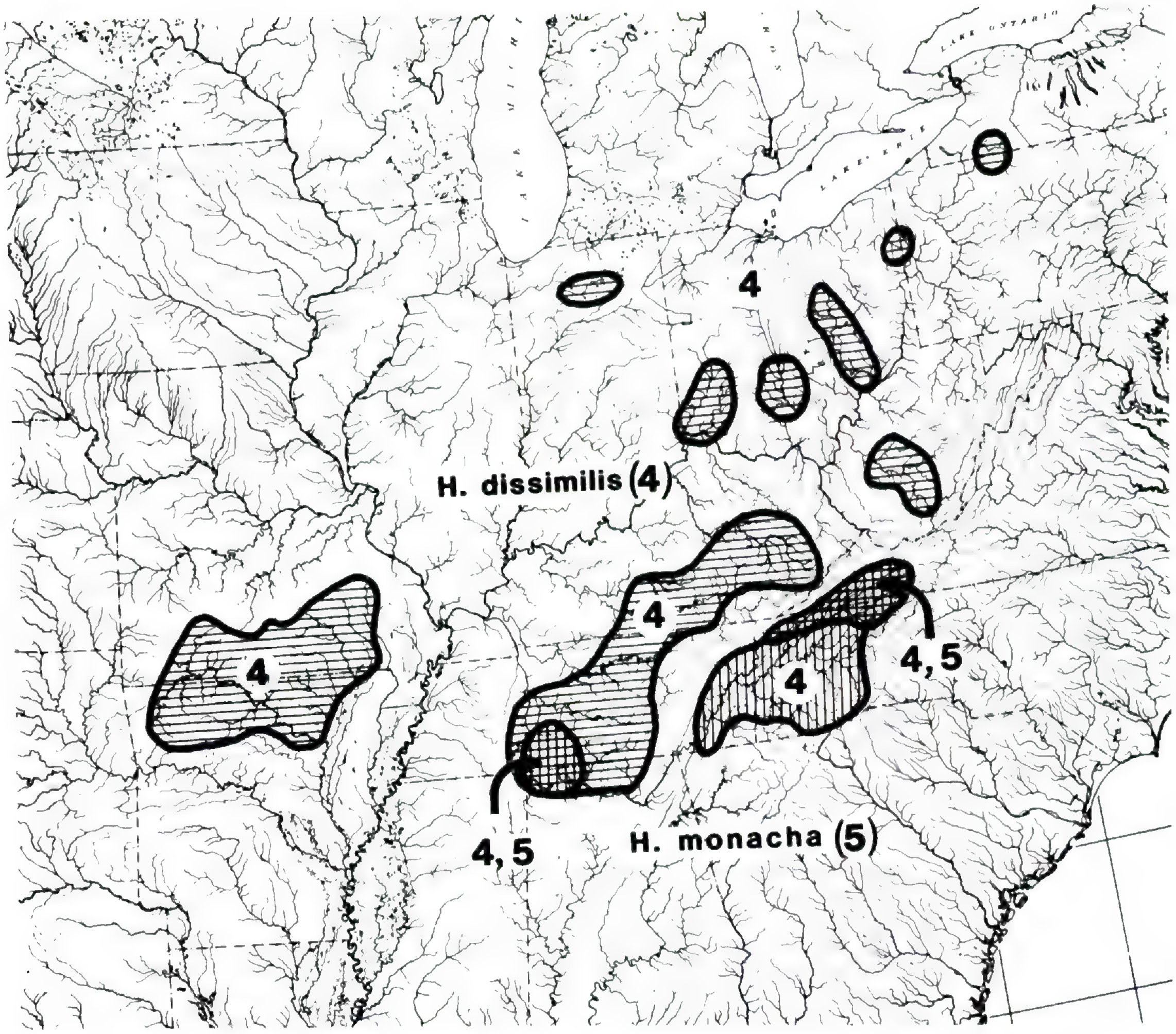

FIGURE 34. Distribution of the remaining species of the *Hybopsis dissimilis* species group (from Lee et al., 1980). Tree: 3+4+5+(1+2). Characters supporting monophyly of the group: (1) an elongate basihyal, (2) stellate barbel morphology, (3) high vertebral count. Character supporting (1+2): distinct lateral blotches on the side of the body. (Characters from Mayden, unpubl. data.)

lection and recombination, might show this relationship if a cladistic analysis was performed on geographic samples of populations of A and B. Mitochondrial DNA has the kinds of evolutionary characteristics suitable for such an analysis (Avise et al., 1979).

Another line of evidence might be developed by considering "ancestral clines," i.e., clines apparently present in ancestors that are retained in descendants (Wiley, 1981). At this level of analysis, does the putative peripheral isolate fit into the pattern of geographic variation exhibited by populations of the supposed ancestor? If so, can we use this as evidence to prefer the scenario in Figure 42b relative to the alternatives? Perhaps if we can show that the characters are derived and heritable or that the pattern indicates a past history of genetic contact, then the species pair is a good candidate for the peripheral hypothesis.

Returning to the *F. diaphanus–E. waccamensis* problem, we note the following. In terms of extrinsic evidence (1) Lake Waccamaw did not exist in the Middle Pleistocene. Thus its present freshwater fish fauna is the result of a colonizing event. (2) The lake is unique ecologically, being a clear, spring-fed lake surrounded by a tannic acid aquatic environment typical of the area. In terms of intrinsic evidence we note that while no detailed analysis of geographic variation has been published, *F. diaphanus* is comprised of two recognized subspecies connected by a zone of integration. The eastern form is "more similar" to *F. waccamensis* than is the northwestern form. Thus what we know about the relationships of

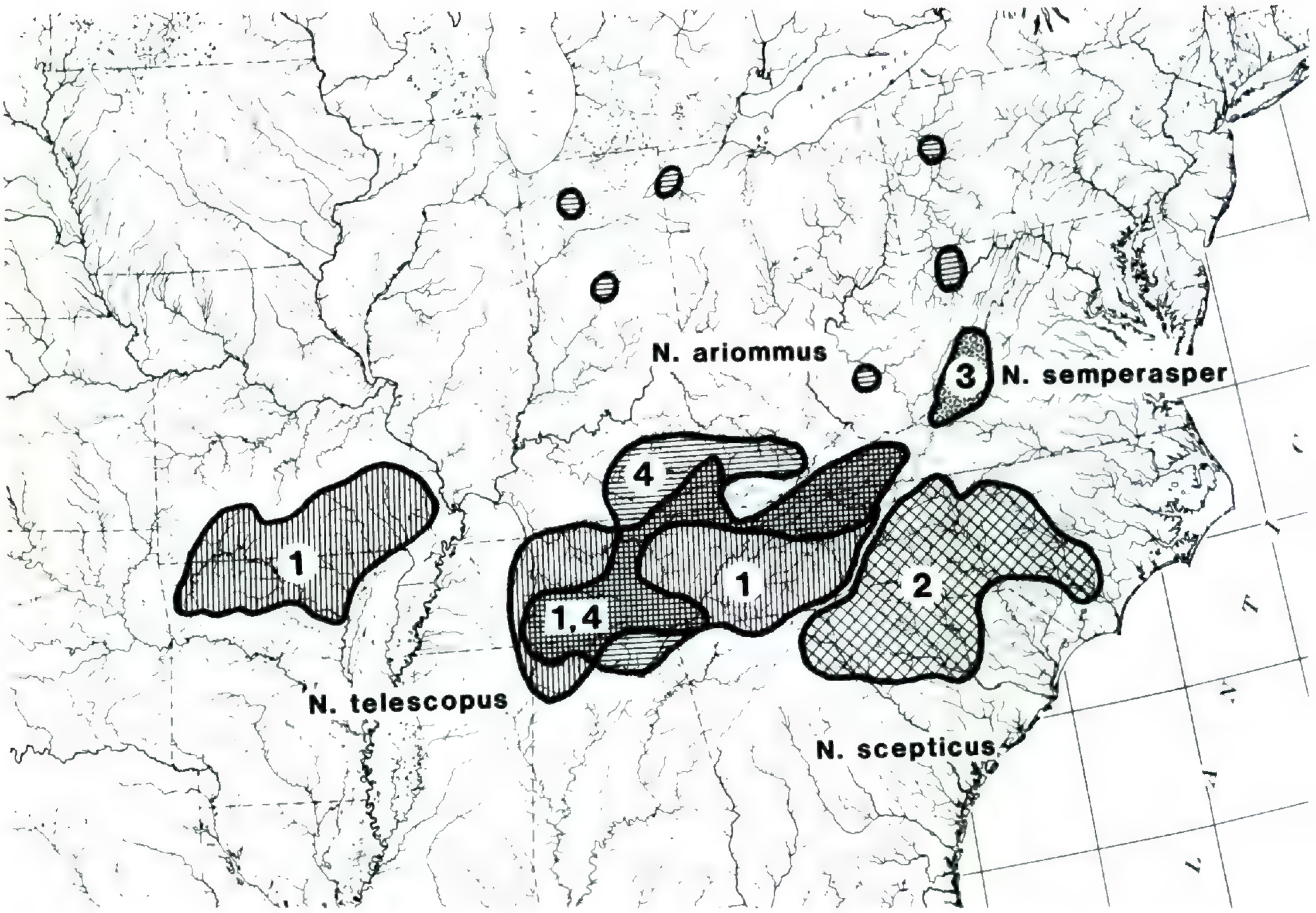

FIGURE 35. Distribution of the *Notropis telescopus* species group (from Lee et al., 1980). Tree: 1+[4+(2+3)]. Characters supporting tree: see Coburn (1982).

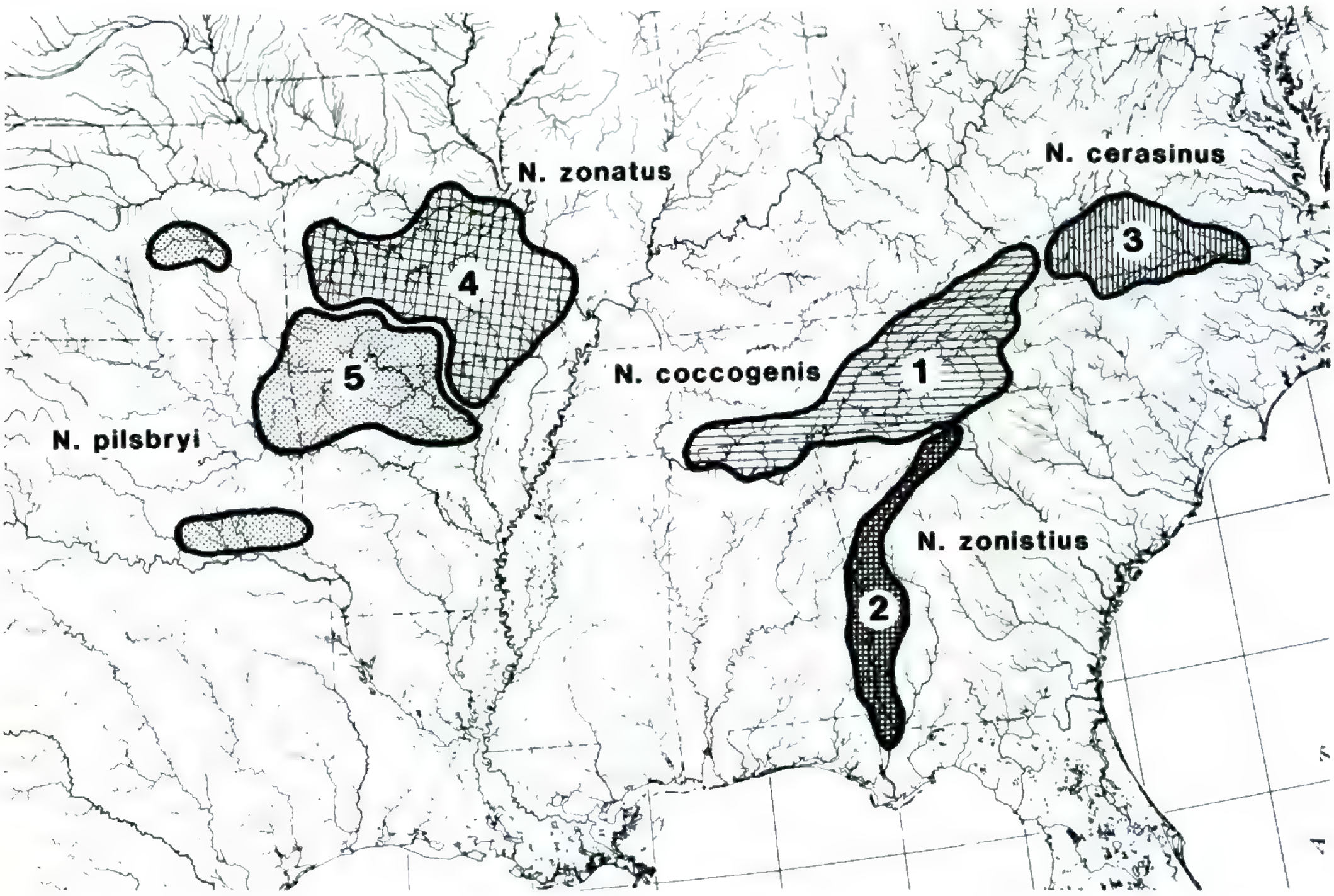

FIGURE 36. Distribution of the *Notropis zonatus–coccogenis* species group (from Lee et al., 1980). Tree: [4+5]+[3+(1+2)]. Characters supporting tree: see Buth (1979).

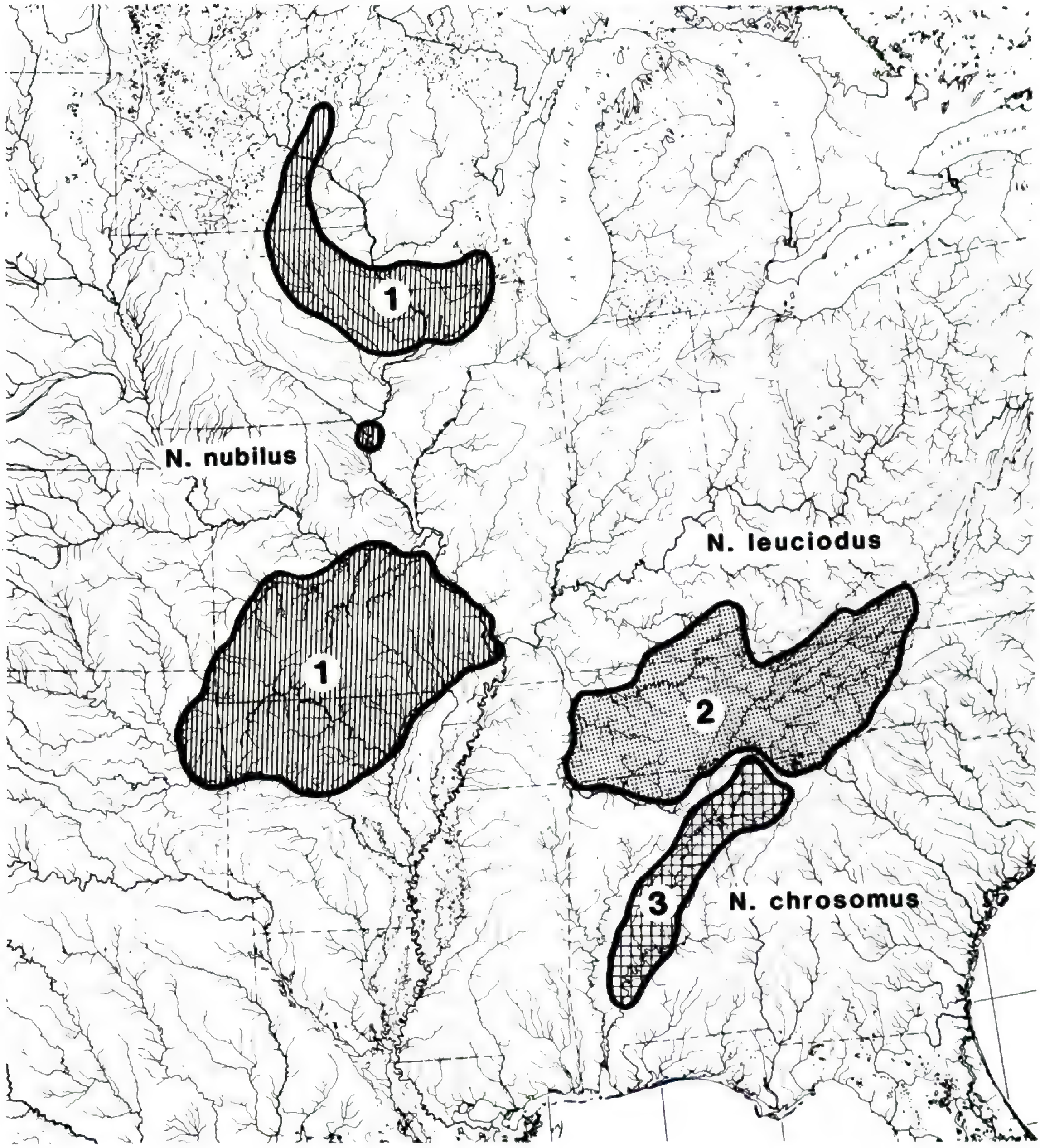

FIGURE 37. Distribution of the *Notropis nubilus* species group (from Lee et al., 1980). Tree: 3+(1+2). Characters supporting monophyly of the group: (1) iridescent breeding colors, (2) dorsolateral pigment pattern on the scales heavily scalloped. Character supporting (1+2): presence of a dashed iridescent predorsal stripe. (Characters from Mayden, unpubl. data.)

the two species does not preclude the hypothesis that *F. waccamensis* is a peripheral isolate derived from *F. diaphanus*.

The problem is that such evidence is relatively weak considering the supposed importance of the phenomenon. In many cases the tentative nature of such speculations are compounded by the fact that the species pair involved is a singular and unique example. In the next section we will suggest that hypotheses of peripheral isolation may be strengthened if we can find additional examples under certain circumstances either in the same clade, or in different clades inhabiting the same region.

Peripheral isolation—multiple speciation events. Single and unique speciation events are

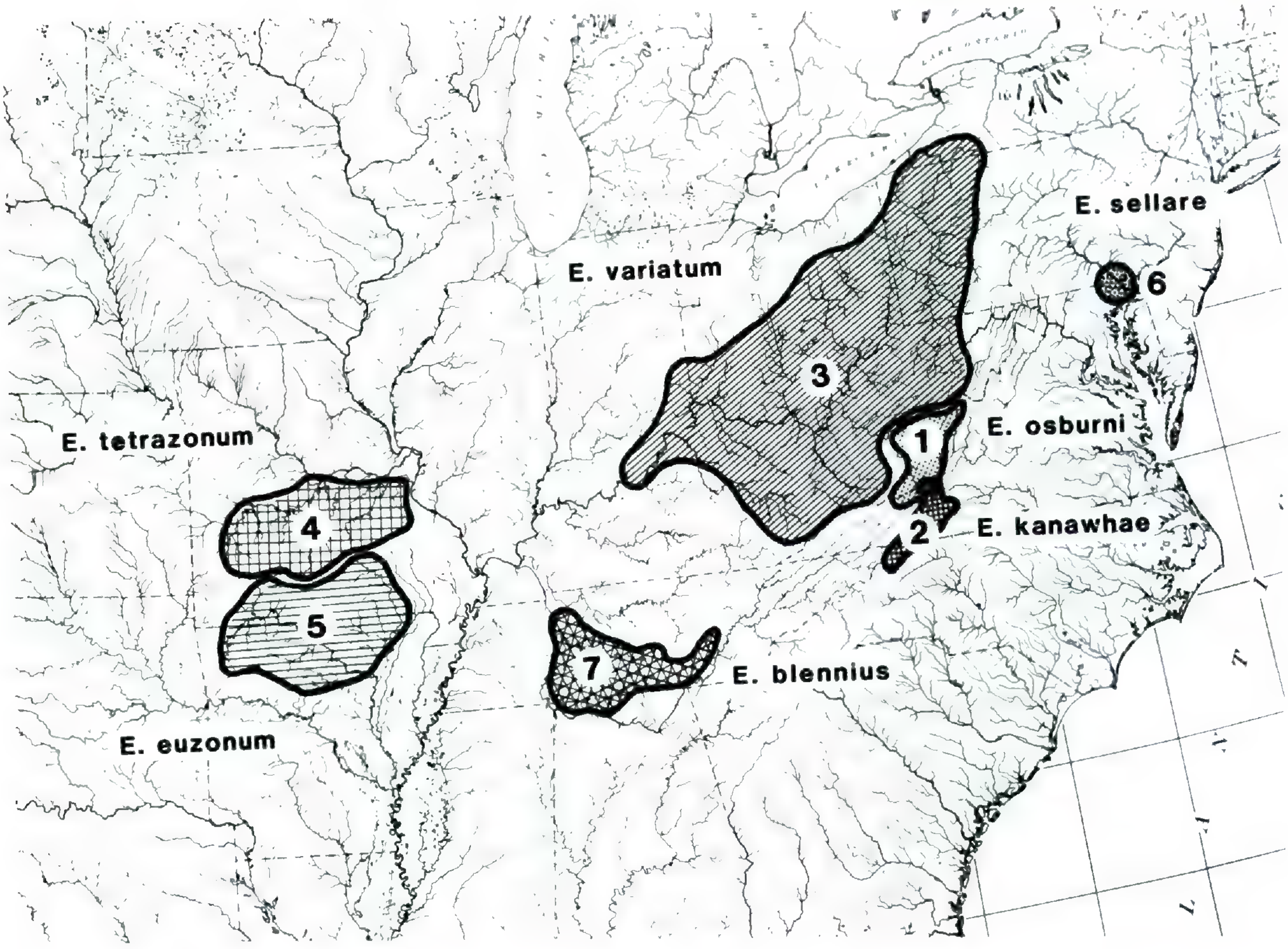

FIGURE 38. Distribution of the *Etheostoma variatum* species group (from Page, 1983). Tree: 7+[[6]+[(3+(1+2))+(4+5)]]. Characters supporting monophyly of the group: (1) fifth infraorbital pore and canal directed dorsally, and (2) large dark dorsal saddles on the body. Characters uniting 1 to 6: (1) anal rays 9, (2) prevomerine teeth present. Characters uniting 1 to 5: (1) breeding tubercles in males and females, (2) brilliant breeding colors. Character uniting (4+5): derived mobility of GPI-2 (100). Character uniting 1 to 3: vertical bars on caudal peduncle continuous ventrally. Characters uniting (1+2): (1) 10 vertical bars on side of body, (2) yellow-gold bar on face. (Characters from Mayden, unpubl. data.)

not easy systems to work with because we lack degrees of freedom to speculate about the possible effects of dispersal, selection, and other phenomena that could lead us to the wrong hypothesis. A clade containing several species, more than one of which had some characteristics of peripheral isolates, or a biota containing an area of endemism inhabited by several suspected peripheral isolates would give us more room to speculate.

Wiley (1981) considered patterns of descent involving peripheral isolation. One case involves an ancestor that "buds off" more than one descendant. Since the two descendants do not share a unique history, they have nothing in common other than sharing an ancestor (i.e., they lack synapomorphies uniting them). If the ancestor remained conservative and if it were treated as a single unit, a trichotomy would be obtained. If the peripheral isolation events were far enough separated in time and the ancestor was evolving, a dichotomy would be obtained. If the ancestor was very widespread and geographically variable, and there were numerous peripheral isolates, a cladistic analysis might show a very complex phylogeny with the population samples of the ancestor appearing on the phylogeny next to or close to peripheral isolates in geographic proximity. We have no such examples in fishes, but if Shaffer's (1984) cladistic analysis of Mexican ambystomatid salamanders is fairly accurate, the phylogenetic pattern he obtained is what we would expect to see. Populations of *Ambystoma tigrinum* (the suspected ancestor, widespread in North America and found in each of the endemic basins of the Mesa Central) appears in the phylogeny interdigitated among no less than 12 species (including both terrestrial and aquatic forms), of very limited range.

The second approach is to search for different

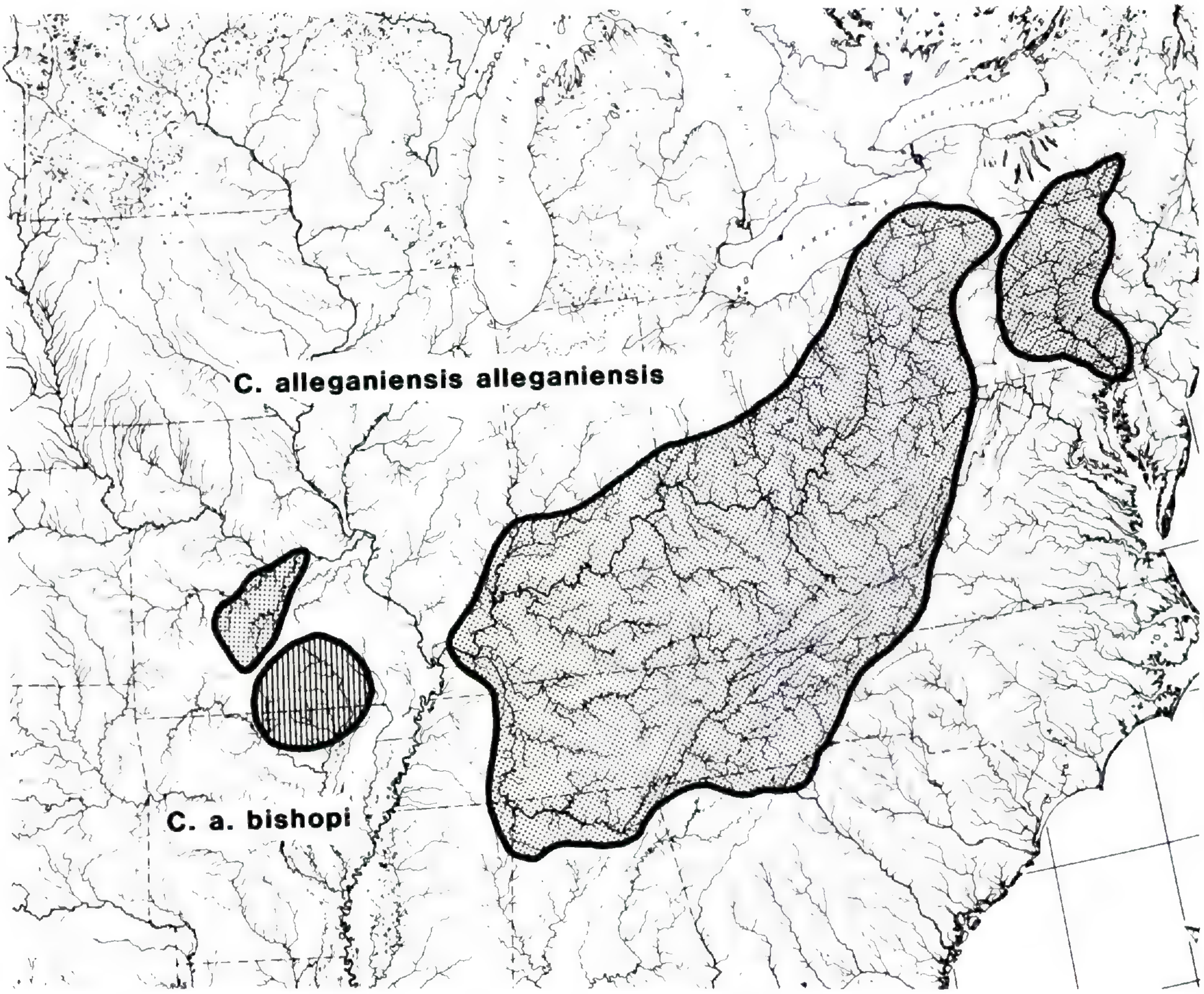

FIGURE 39. Distribution of *Cryptobranchus alleganiensis* (from Conant, 1975).

groups that have endemics in the same restricted area. We can then use the methods of vicariance biogeography to examine the phylogenetic and biogeographic relationships of the endemics to their sister species. For example, Lake Waccamaw has three endemic species of fishes, each with a widespread sister species. One is *F. waccamensis*. The second is *Menidia extensa* (a silverside). It is related to the wide-ranging coastal species *M. beryllina*. The third is *Etheostoma perlongum*, a darter related to *E. omstedi*. The distributions of the three species pairs are shown in Figure 43. Note that the three widespread species have little in common, their ranges do not coincide, they have different ecologies, and they are very distantly related. Given these observations, coupled with the relatively late origin of Lake Waccamaw, it is improbable that the scenarios in Figure 42c, d, and e can explain a distributional pattern in which there is geographic congruence of three unrelated endemics but little congruence between the closest relatives of these endemics other than the fact that each is found around the lake. The best explanation seems to be Figure 42b. Finally, we note that Lake Waccamaw has a diverse fish fauna (Hubbs & Raney, 1946), and the vast majority of species have not speciated in the lake. This indicates that while unique ecological circumstances might promote differentiation; differentiation is not an automatic consequence of changing the ecological parameters a population finds itself in.

The North American fish fauna contains many species whose distributions suggest peripheral isolation, especially among darters and minnows. For example, *Notropis procne* is a widespread species while its sister species, *N. mekistocholas* (Snelson, 1971) has a limited and peripheral distribution (Fig. 44). We might entertain the hypothesis that the origin of *N. mekistocholas* involved peripheral isolation and that *N. procne* is the extant ancestor. However, our

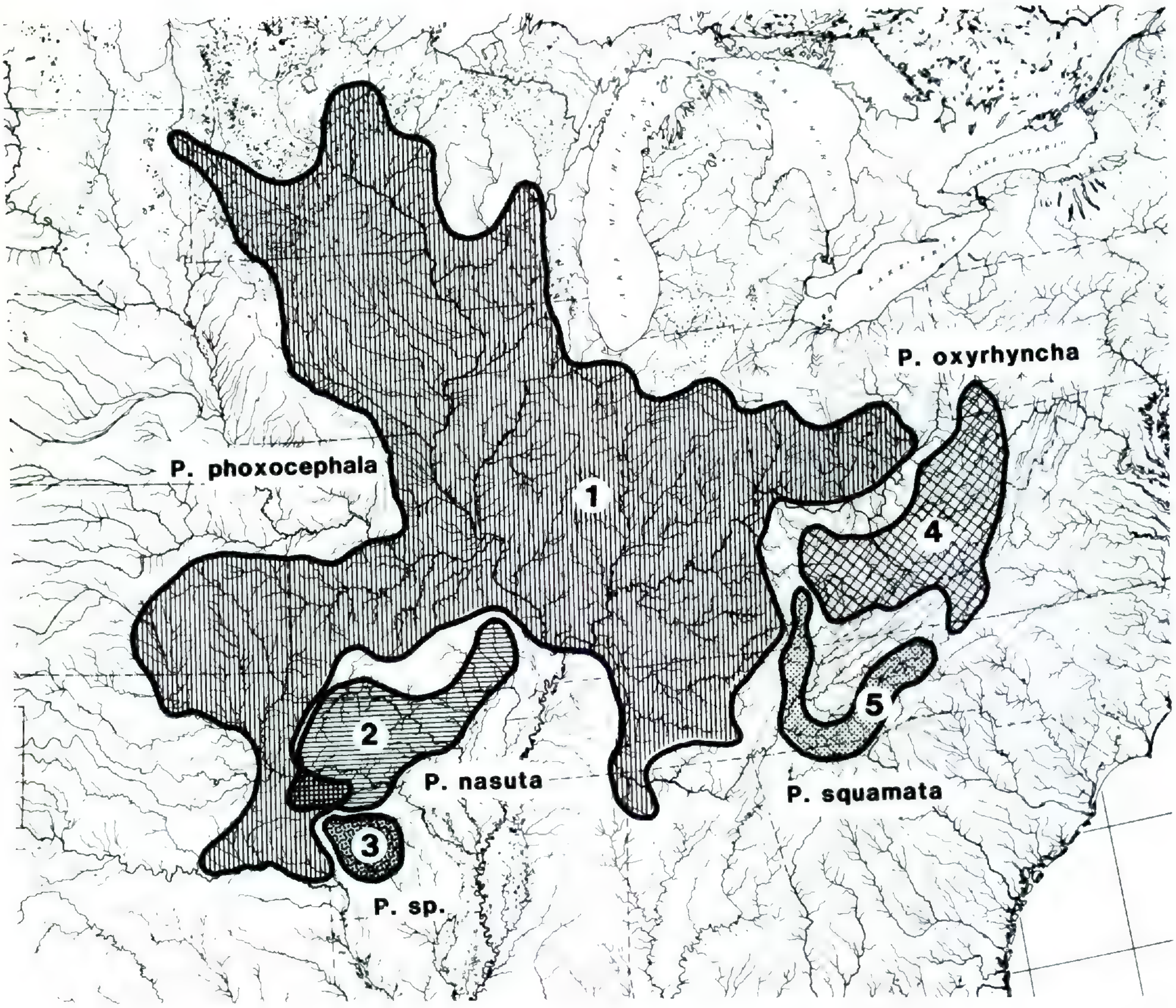

FIGURE 40. Distribution of subgenus *Swainia* genus *Percina* (from Page, 1983). Tree: 1+[(2+3)+(4+5)]. Characters supporting tree: see Page (1983) and Mayden (1985).

lack of knowledge of the cladistic relationships among populations of the hypothesized ancestor coupled with our lack of knowledge of the closest relative(s) of the species pair limits our ability to follow up our analysis. We can neither test the proposition by showing that some population or populations of *N. procne* are cladistically nearer the descendant for some characters nor can we show that the putative descendant conforms to the deviation rule of Hennig (1966).

Perhaps as important as finding criteria from which one can use phylogenetic analysis to corroborate hypotheses of peripheral isolation is to find cases in which phylogenetic analysis causes rejection of the hypothesis or indicates a need for collection of additional data. For example, *Fundulus albolineatus* and *F. julisia* are two obvious candidates for the peripheral isolates hypothesis and are surrounded by a possible ancestor, *Fundulus catenatus* (Fig. 32). However, what little we know of the relationships of this group indicates that *F. catenatus* is more closely related to *F. stellifer,* and thus these species do not conform to the expected pattern of peripheral isolates and their ancestors (Wiley, in press; data from Williams & Etnier, 1982).

The continuum of allopatric speciation from large-scale vicariance and peripheral isolation is apparent when we consider "mini-vicariance." Mayden (1985) has examined several species found in the Ouachita Highlands whose closest relatives inhabit the surrounding lowlands. These include eight species of fishes: two minnows (*Notropis perpallidus* and an undescribed species), two madtom catfishes (*Noturus lachneri* and *N. taylori*), four darters (*Etheostoma pallididorsum, E. radiosum, Percina pantherina,* and an undescribed species). In addition there are six species

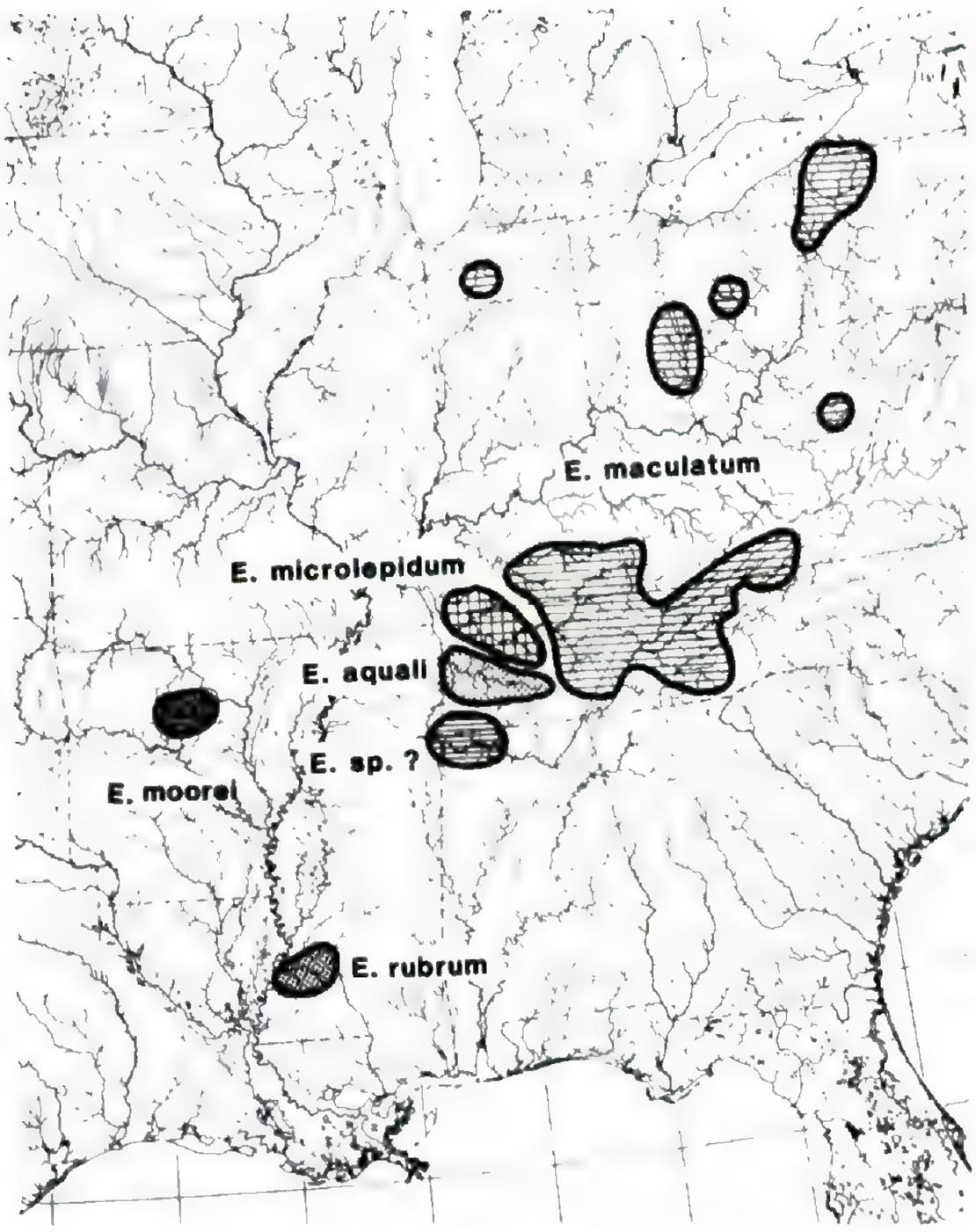

FIGURE 41. Distribution of the *Etheostoma maculatum* species group (from Williams & Etnier, 1982 and Page, 1983). Tree: relationships unresolved.

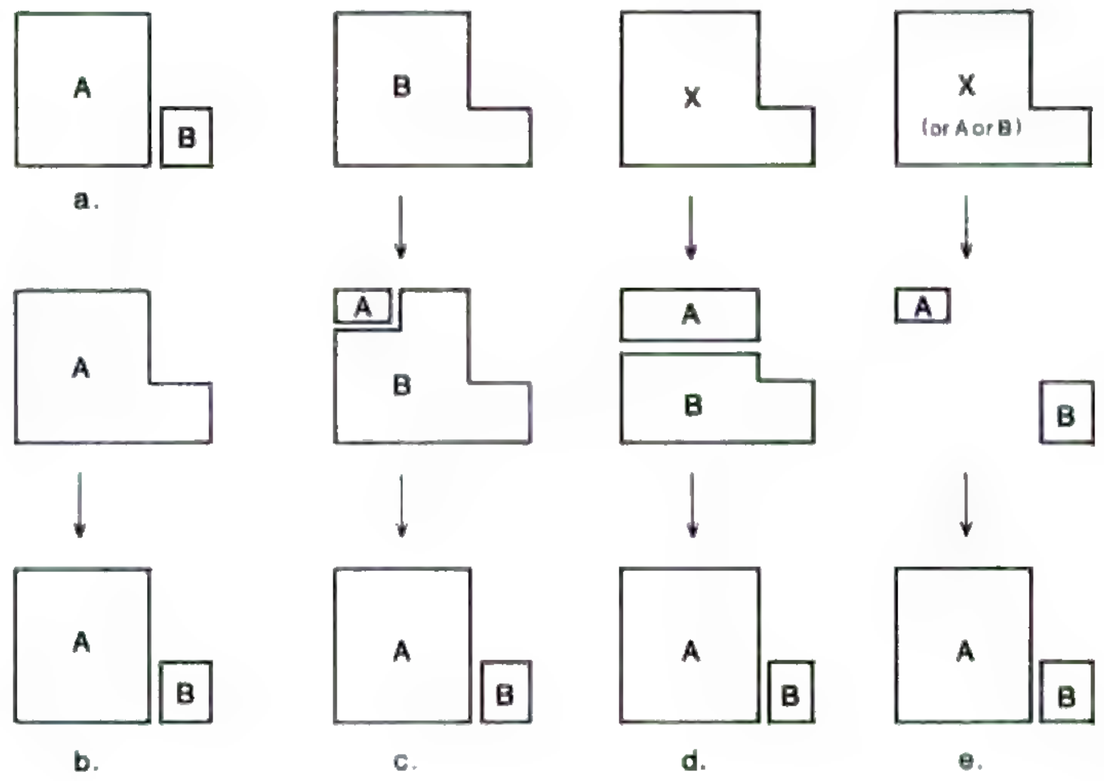

FIGURE 42. Scenarios concerning the evolution of species A and B.

of crayfishes: *Orconectes leptogonopodus, O. menae, Procambarus ouachitae, P. parasimulans, P. reimeri,* and *P. tenuis* (for references see Mayden, 1985). The congruence observed points to a common vicariance event involving the Ozark Highlands, possibly associated with the dissection of the Interior Highlands by the Arkansas River, and a common event with species surrounding or south of the highlands. The fact that a relatively small geographic region was involved makes this pattern a candidate for "vicariant peripheral isolation."

There are many North American fishes that have restricted distributions, making them candidates for the peripheral isolation model. While some can be dismissed because of age or obvious extinction patterns, others cannot be so lightly dismissed. Our major problem, however, is that we lack the phylogenetic information needed to do the necessary kinds of analyses to test the model.

ALLO-PARAPATRIC AND PARAPATRIC SPECIATION

Allo-parapatric speciation occurs when two populations of an ancestral species become disjunct, differentiate to some degree during the time they are allopatric, become sympatric in a limited area, and complete their divergence because of interactions in the zone of sympatry. Parapatric speciation occurs when two populations attain lineage independance while maintaining a narrow zone of contact (see Wiley, 1981, for summaries of both models). Both models are hard to test, at least in fishes. An investigator postulating the allo-parapatric model must demonstrate that (1) the contact zone is a secondary zone achieved after a disjunction, and (2) that the differences observed between the species have either been evolved or "perfected" because of the interactions within the contact zone. An investigator postulating the parapatric model must demonstrate that (1) the contact zone is a primary zone, and (2) the differences we observe have been achieved in spite of the contact between the two species. The simple observation of the presence of the contact zone is not sufficient. Testability is confounded because except for the presence of the contact zone itself, the phylogenetic and biogeographic predictions we can derive from both models are similar to those we can derive from the various modes of allopatric speciation (Wiley, 1981).

We do not have examples of either of these modes of speciation in the North American fish fauna. There are several reasons for this. First, it has been a tradition among North American ichthyologists to favor a rather strict definition of the biological species concept. Thus nominal taxa showing even limited interbreeding within a contact zone are usually considered as a single species and the possibility of either mode operating is never considered. Second, freshwater fishes are confined to the streams they inhabit

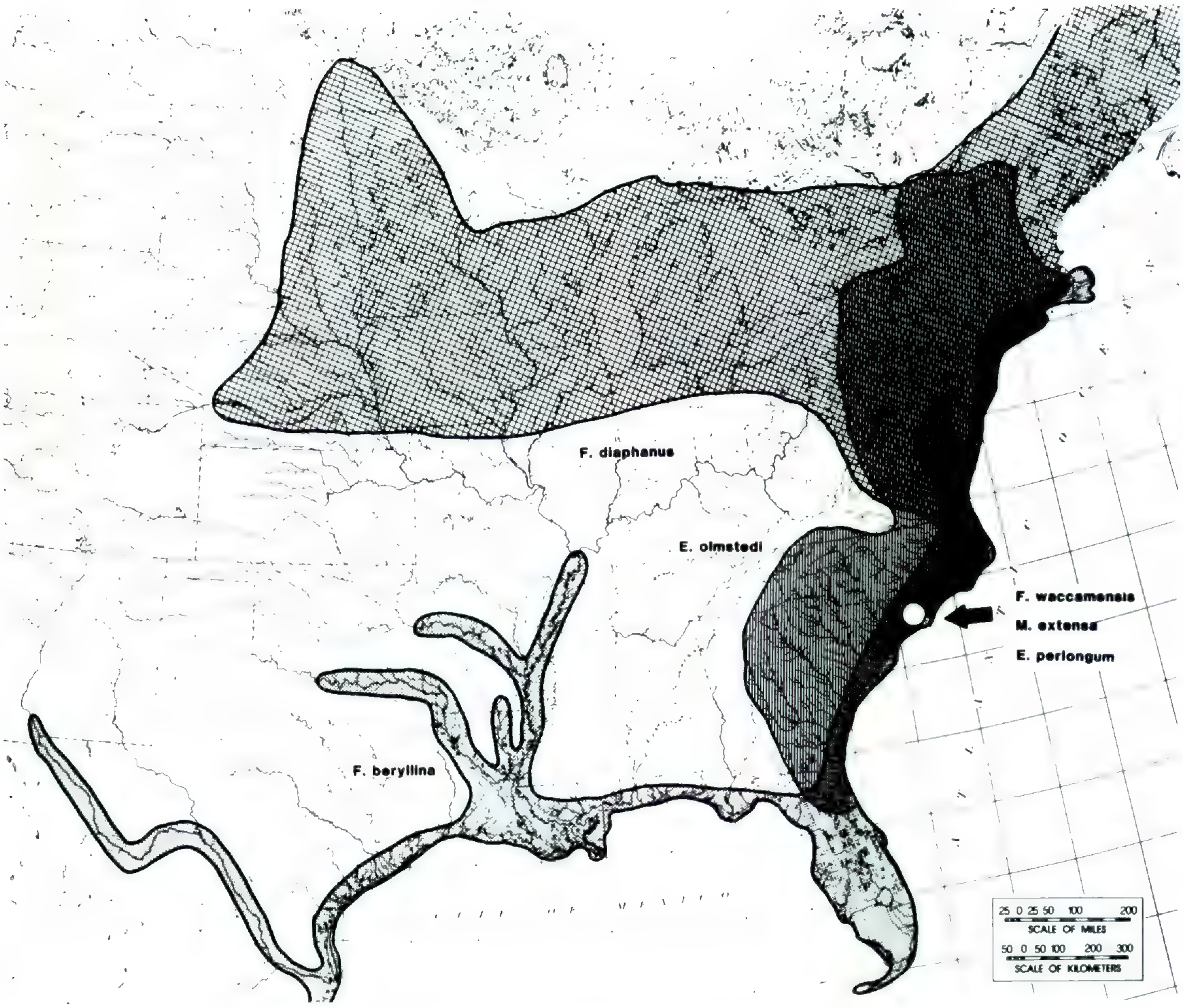

FIGURE 43. Distributions of three species endemic to Lake Waccamaw, North Carolina, and their widespread closest relatives (from Lee et al., 1980).

and this limits the possibilities for establishing contact zones and enhances the possibilities for allopatry between drainages. Thus, parapatric and allo-parapatric speciation would be expected to be largely confined to within-drainage systems situations. Third, we of the ichthyological community simply have not been looking for evidence of either mode because we tend to think "allopatrically."

STASIPATRIC SPECIATION

Although stasipatric speciation has frequently been considered synonymous with parapatric speciation, we restrict it to a mode of speciation involving chromosome mutations coupled with some mechanism such as drift or meiotic drive to fix the mutation in a small population, following the model presented by White (1978). We have no examples of this mode of speciation in the North American fish fauna and we see no hope of finding examples until such time as methods for banding fish chromosomes are generally made available.

SYMPATRIC SPECIATION

As discussed by Wiley (1981), there are several modes of speciation that do not depend on any degree of geographic subdivision and thus can be termed "sympatric" modes. There are no examples of North American fishes that show an ecological mode of sympatric speciation. There are examples involving hybridization and sexual shifts that have produced unisexual species. These include two well-documented examples.

Poecilia formosa is a gynogenetic species (Hubbs, 1964) found in northern Mexico and

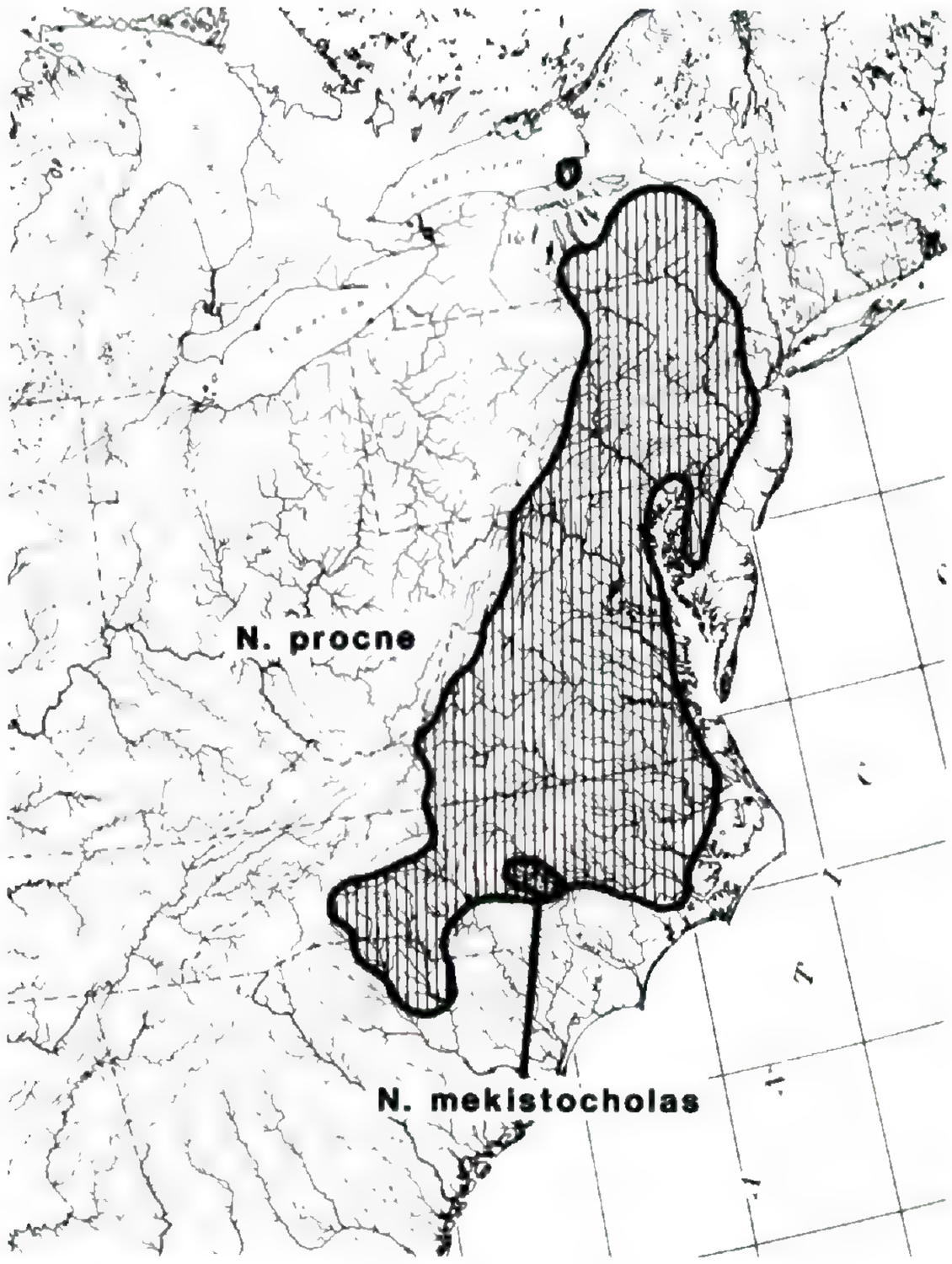

FIGURE 44. Distribution of *Notropis procne* and *N. mekistocholas* (from Lee et al., 1980).

southern Texas. Hubbs and Hubbs (1932) suggested that this species originated by hybridization between the bisexual species *P. latipinna* and *P. sphenops*. [Species composition of the *P. sphenops* complex is not clear (Schultz & Miller, 1971) and the species involved in the hybridization event could have been *P. mexicana* or *P. sphenops*.] Although *P. latipinna* and members of the *P. sphenops* complex are in the same subgenus, they are not considered very close relatives.

Menidia clarkhubbsi is a unisexual species of silverside found at three different locations in Texas (Echelle & Mosier, 1982). Echelle and Mosier (1982) hypothesized that the species arose via hybridization between two species, *M. beryllina* and *M. peninsulae*. The parental species are not sister species. *Menidia beryllina* is more closely related to *M. extensa* than to *M. peninsulae* (Johnson, 1975).

In addition, there are at least five "forms" of the topminnow genus *Poeciliopsis* that are composed of parthenogenic females (Schultz, 1967; Moore et al., 1970). However, the nomenclature and relationships of these forms are not clear (R. R. Miller, pers. comm.). They may be examples of species derived from hybridization and sexual shifts, sexual shifts alone, or morphs within their respective species.

DISCUSSION AND CONCLUSIONS

Analysis of phylogenetic and biogeographic patterns of descent and attempts to correlate these patterns with modes of speciation has hardly begun. Our attempts with selected North American fishes is a preliminary effort, but they suggest that such correlations can be made. Our first example, the Northern Gulf Coast, suggests a pattern of large-scale allopatry (model I) involving several clades. We note that the number of species involved is small relative to the number of species inhabiting the region and that the groups themselves do not comprise a "biota" in the sense discussed by vicariance biogeographers (Fig. 45). Further, not all speciation followed a common pattern. Our second example, the Central Highlands, can only be considered a counter example. We observe vicariance without consequent speciation. Apparently the species inhabiting the regions were present before the vicariance event that caused the disjunction of the fauna. However, the effects of vicariance can be seen within the Interior Highlands in a pattern of "minivicariance" in the Ouachita Highlands.

Our attempt to corroborate the peripheral isolation hypothesis proposed by previous workers for three species endemic to Lake Waccamaw met with success, but although other biogeographic patterns involving putative ancestors and descendants are suggestive of this phenomenon, we lack the phylogenetic and biogeographic information necessary to pursue such hypotheses. Two examples of multiple peripheral isolation were examined. In one (*Fundulus catenatus, F. julisia,* and *F. albolineatus*) hypotheses that the two species of restricted distribution are peripheral isolates of the wide-ranging species are not corroborated because the wide-ranging species, *F. catenatus,* is more closely related to *F. stellifer.* This does not falsify either hypothesis, but it does require that we must minimally entertain the idea that *F. catenatus* has evolved anagenetically and given rise to *F. stellifer* after the origin of the two peripheral isolates if it is, indeed the ancestor. (But if this is true, would the species that gave rise to *F. albolineatus* and *F. julisia* be *F. catenatus*?) The other example, species of ambystomatid salamanders of the Mesa Central seems to offer a clearer picture, but we need examples among fishes.

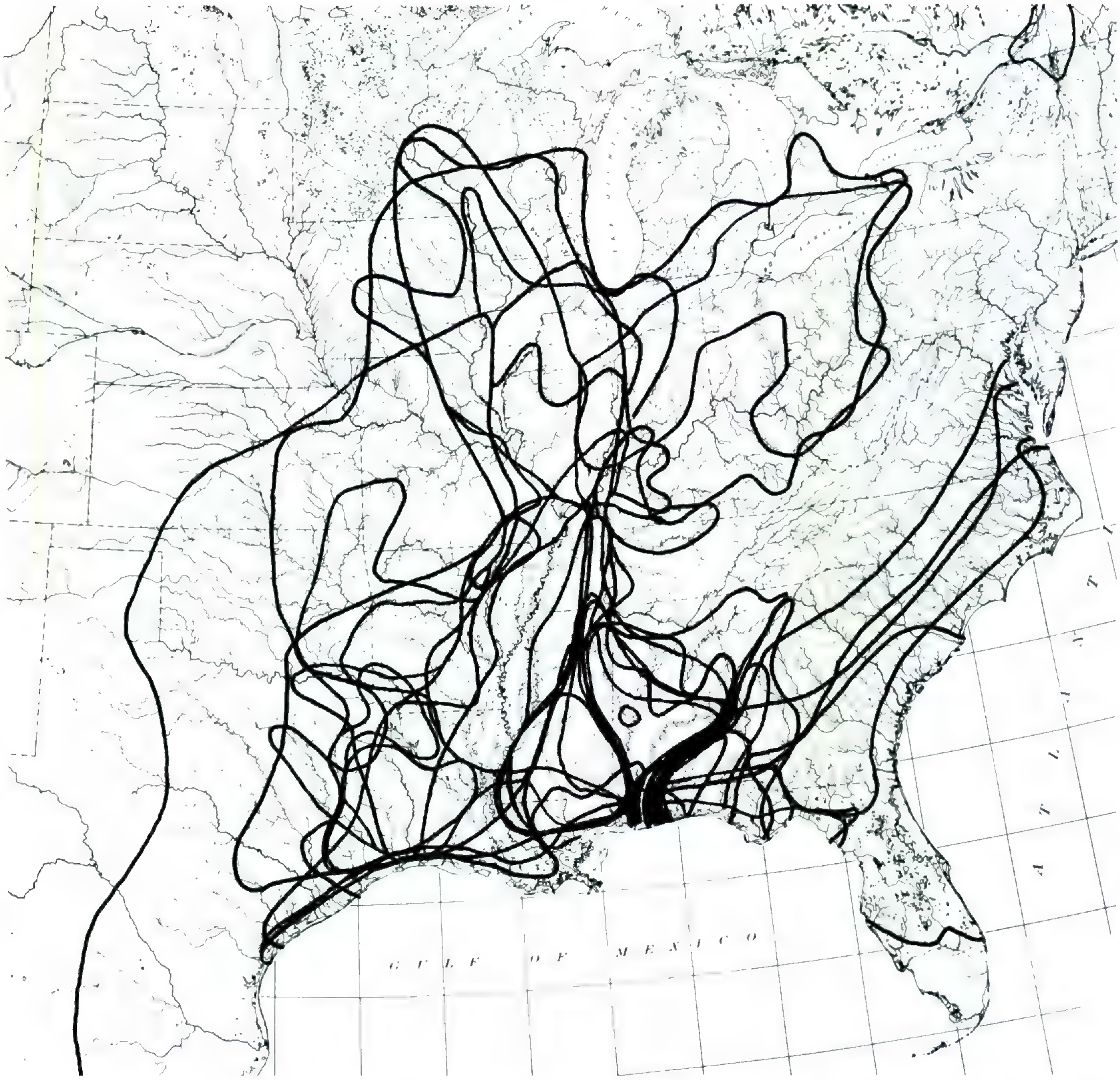

FIGURE 45. Summary map of distributions of taxa from the Central Gulf Coast and adjacent regions considered in this paper.

We were not able to provide evidence for either allo-parapatric or parapatric speciation. It is possible that, because freshwater fishes are confined to their streams, the opportunity for either mode to operate is restricted. Perhaps studies of coastal species where this restriction is not present will provide an opportunity to demonstrate these modes of speciation.

The only sympatric mode of speciation well documented in the North American fish fauna is speciation via hybridization associated with asexual or gynogenetic reproduction of all-female descendants. In neither case were the species of hybrid origin the result of hybridization between closest relatives.

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GEOLOGICAL HIERARCHIES AND BIOGEOGRAPHIC CONGRUENCE IN THE CARIBBEAN[1]

DONN E. ROSEN[2]

ABSTRACT

If it is agreed that an understanding of biohistory in some ways is tied to an understanding of geohistory, then one might also agree that what is needed is a precise means of specifying how a given biohistory is explicitly tied to a particular geohistory. The constraint in this type of analysis is the branching diagram, or cladogram, that permits a precise comparison of geographic area cladograms to demonstrate congruence between the cladistic message from biology with the cladistic message from geology. A proposal for identifying these cladistic constraints is given using a comparison of several different historical geologies of the Caribbean region as an example that contrasts with the constraints used by previous biogeographies in which an a priori notion of process, e.g., dispersal or extinction, was used to direct the outcome of biogeographic analysis.

Whether espousing dispersalism (Darlington, 1957) or vicariism (Croizat, 1958, 1962), biologists have always assumed that the distributions of organisms in some way reflect the nature of the world's geologic history. It was, thus, implied that an understanding of biohistory is tied to an understanding of geohistory. In the Darwinian-Darlingtonian tradition the relevant geohistory was assumed to be one of stabilism necessitating an interpretation of biohistory as one of active or passive dispersal. In other words, so long as the continents stood still something had to move to account for the occurrence of closely related organisms spanning large water gaps. Thus were invoked temporary land bridges suitable for crossing ocean barriers, birds with feet and feathers to which seeds and small animals would adhere during their transoceanic flights, and menageries supported on floating debris that was spewed into the ocean's currents from river mouths and deltas.

The difficulties inherent in these scenarios of a haphazard biohistory are apparent in Darlington's (1957) hypothesis that ostariophysans arose in central Asia and made their risky way along ephemeral freshwater routes to the southern continents without leaving a trace of these great migrations. But the hypothesis of a steadfast geography and a dancing biota was deemphasized after the theory of plate tectonics was elaborated.

Since most biologists had a penchant for believing that geologists had a special hold on the truth, the acceptance of continental drift caused some of these biologists to shift into reverse strategy of proposing that it was the geography that moved while the organisms got carried about to their new longitudes and latitudes. Other biologists (Darlington, 1965; McDowall, 1971; Briggs, 1984) tried and still try to rescue the past by agreeing that the geography did in fact move but that the timing of these great events was wrong in relation to the ages of the biotas. Such attitudes might invoke the ages of fossils to show that all the taxa are too young to have been influenced by the geographic cataclysms. This view involves two assumptions, both wrong at some level: 1) that fossils can tell us how old a taxon is and 2) that the ages of the geologic events have been correctly assigned. The first assumption is wrong because fossils give a minimum rather than maximum age of a taxon, and the second assumption is put into question by recent age reassignments. For example, parts of the Caribbean which were originally supposed to have been moving along a transform fault at the moderate rate of 2 cm per year (Kellogg & Bonini, 1982) are now believed to be moving at the brisker pace of 4 cm per year (Sykes et al., 1982; Wadge & Burke, 1983), thus doubling the rate of motion and halving the ages of the events associated with translocation. But these relations leave us still at the mercy of general supposition when what is needed is some precise means of specifying that this biohistory is tied explicitly to that geohistory. This still unrealized need for precision is supplied by another conceptual revolution that, in terms of time spans involved in human intellectual history, might be said to have occurred more

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or less simultaneously in systematics and biogeography.

This revolution has been called cladistics, the science of character analysis and the use of branching diagrams. Its premises permit precise comparisons between biological and geological systems (e.g., Rosen, 1978). The general objective of cladistics is to discover congruence between the two that constrains historical explanation.

In the Darwinian tradition in biogeography it is dispersal that was the constraining concept, requiring an interpretation of the history of life in space contrary to what the data of life suggested. Leon Croizat (1958, 1962) was one of the pioneers who recognized that the biological data tell their own story, which can be at odds with a stabilist geology. Now that stabilist geology has been rejected in favor of a concept of mobilism, some biogeographers (Nelson & Platnick, 1981; Wiley, 1981) accept that biology has an independent story to tell about the history of the world. It is this independence of biological from geological data that makes the comparison of the two so interesting because it is hard to imagine how congruence between the two could be the result of anything but a causal history in which geology acts as the independent variable providing opportunities for change in the dependent biological world. The comparison becomes especially interesting if there is a congruence among geohistories based on different approaches to the geographic problem, and if there is a congruence among cladistic relations of different taxa with respect to the same geographic areas. The specific questions are: 1) do the members of different monophyletic groups of organisms have the same relations to each other with respect to geographic regions in which they are endemic and is their congruence with respect to these areas non-random; and 2) does this non-random congruence of different groups of organisms correspond to a branching diagram that represents part of the history of some geographic region? The constraint in these comparisons is the branching diagram rather than a process assumed to be of causal importance.

In 1976 and 1978 I suggested a history for the Caribbean land and water that, at a rather general level, is consistent with the present distributions of plants and animals in the region including the Antilles, Central America, northern South America, and the southeastern and southwestern United States. The 1976 proposal, which was based largely on a descriptive history by Malfait and Dinkleman (1972) and Tedford (1974), was questioned by Pregill (1981) whose claim was that there is no geologic evidence warranting such a proposal. This claim was critically evaluated recently by Hedges (1982) who disagreed with Pregill on the grounds that ample geologic data had been available for some time in support of the Malfait and Dinkleman-Tedford theory (he cited 13 literature sources). Since the time of Hedges' reply to Pregill, I became aware of several other accounts of Caribbean history based on a variety of geologic data sources (Birnie, 1977: movement along major fault zones; Pindell & Dewey, 1982: plate contour matching and paleomagmatic data; Kellogg & Bonini, 1982: gravity data, seismic profiles, radiometric data, and earthquake data; Sykes et al., 1982: slip vectors of shallow earthquakes and other seismic data; Wadge & Burke, 1983: reconstructing plate motions by closing the Cayman Trough along its bounding transform faults). It is apparent, therefore, that Pregill was operating with a different set of constraints, namely, that the biota is recently distributed by means of dispersal. Hence, no number of geologic accounts or amount of data would be expected fundamentally to alter his position. My constraint is the cladogram and how it describes relationships of taxa and areas. What I propose is to divide the historical geology of the Caribbean into the minimum number of time periods in which different geologic theories agree on the geographic contacts between different areas and the severing of those contacts. In this way I have covered four main periods spanning 165 million years.

Caribbean History

As I interpret the geological literature the following events took place in Caribbean geohistory; some prefatory remarks are in order.

There are two basic kinds of theories about the history of the Caribbean: 1) those of Salvador and Green (1980) (Figs. 1–9) and Anderson and Schmidt (1983) (Figs. 10–16). These describe a north–south expansion of the Gulf-Caribbean region by the latitudinal displacement of North and South America. Both of these are primarily pre-Cenozoic theories that focus principally on the opening of the Gulf of Mexico so that the detailed placement of the Greater Antilles is secondary in importance. 2) All remaining theories, as exemplified by (Figs. 17–29) Malfait and Dinkle-

FIGURE 1. The Gulf of Mexico and Caribbean region in the Kimmeridgian (143 Ma) according to Salvador and Green (1980). This, and Figures 2–9, is one of two pre-Cenozoic theories focusing primarily on the opening of the Gulf, and is based on the notion that the Caribbean, like the Gulf, was created by north–south spreading or separation of North and South America. It is distinguished by proposing an origin of Cuba from volcanism along a northern South American transform fault and the gradual shift northward toward the Bahama Bank of Cuba. Other Greater Antillean, and the Lesser Antillean components are also viewed as having in situ volcanic origins, although the Beata Ridge is depicted as a volcanic chain of which Hispaniola is the most northerly element. Black dots represent primary sites of volcanism. Vertical hatching is land; cross-hatching is shallow-water shelves with sedimentary deposits; heavy lines with half arrows are transform faults; and heavy lines with solid arrows are subduction zones. Only the main areas of volcanism are shown by the solid dots.

man, and Tedford (see Rosen, 1976), Pindell and Dewey (1982), Sykes et al. (1982) (Figs. 30–33), Wadge and Burke (1983), and Dickinson and Coney (1980) (Fig. 34), describe longitudinal displacement events of land and sea floor that are primarily Cenozoic and focus principally on the Caribbean heartland, particularly the origins and movements of the Antillean islands. Readers of these two kinds of historical geologies will notice immediately that the latitudinal expansion theories place the origin of the Greater Antilles along the northern edge of South America, not unlike the older theory of Vandel (1972), whereas the longitudinal displacement theories identify the main Antillean islands as part of an ancient island arc that connected northern Central America (Yucatan) with northwestern South America. Although seemingly contradictory theories of Caribbean history, the consequences of the two theories in terms of the sequence of land connections and disconnections are similar. Their common elements include: 1) contact between North and South America via a proto-Greater Antilles; 2) Cenozoic longitudinal displacement of the Antilles; 3) hybridity of Hispaniola and contact of central Hispaniola with eastern Cuba; 4) approximation of eastern Cuba with Florida and western Cuba with northern Central America (Yucatan) at some stage; 5) secondary closing of the Central American, South American water gap; 6) motion of the Chortis block (Honduras and Nicaragua) along a transform fault (= Motagua-Polochic fault and Cayman Trench) with comparable motions of the Greater Antillean elements.

Although both theories accept a later origin for lower Central America connecting Honduras and Nicaragua with Colombia, in Pindell and Dew-

FIGURE 2. The Gulf of Mexico and the Caribbean region in the Berriasian (132 Ma) according to Salvador and Green (1980). At this stage some east–west translocation is postulated at the western margin of the Caribbean region (note the position of Honduras and Nicaragua, H-N, and compare with subsequent figures) although a north–south expansion is still considered primary.

FIGURE 3. The Gulf of Mexico and the Caribbean region in the Berremian (117 Ma) according to Salvador and Green (1980).

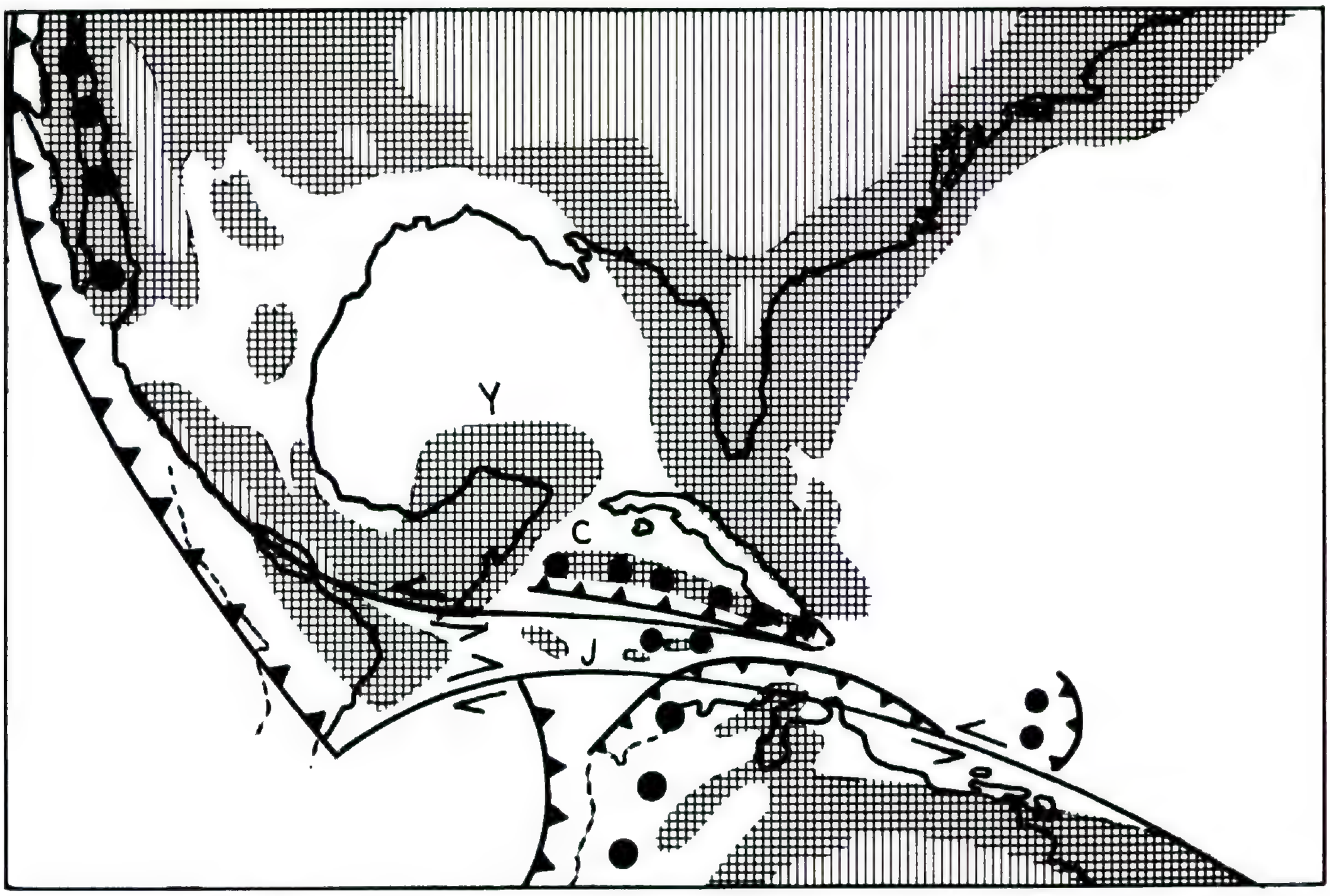


FIGURE 4. The Gulf of Mexico and Caribbean region in the Cenomanian (93 Ma) according to Salvador and Green (1980). Jamaica (J) is depicted as a consequence of submarine volcanism and Hispaniola is shown just to the east of Jamaica with a small subaerial component.

FIGURE 5. The Gulf of Mexico and the Caribbean region in the Maastrichtian (70 Ma) according to Salvador and Green (1980). The outlines of all of the Greater Antillean islands are now shown, with the western, subaerial part of Cuba (C) in contact with the Yucatan (Y) platform.

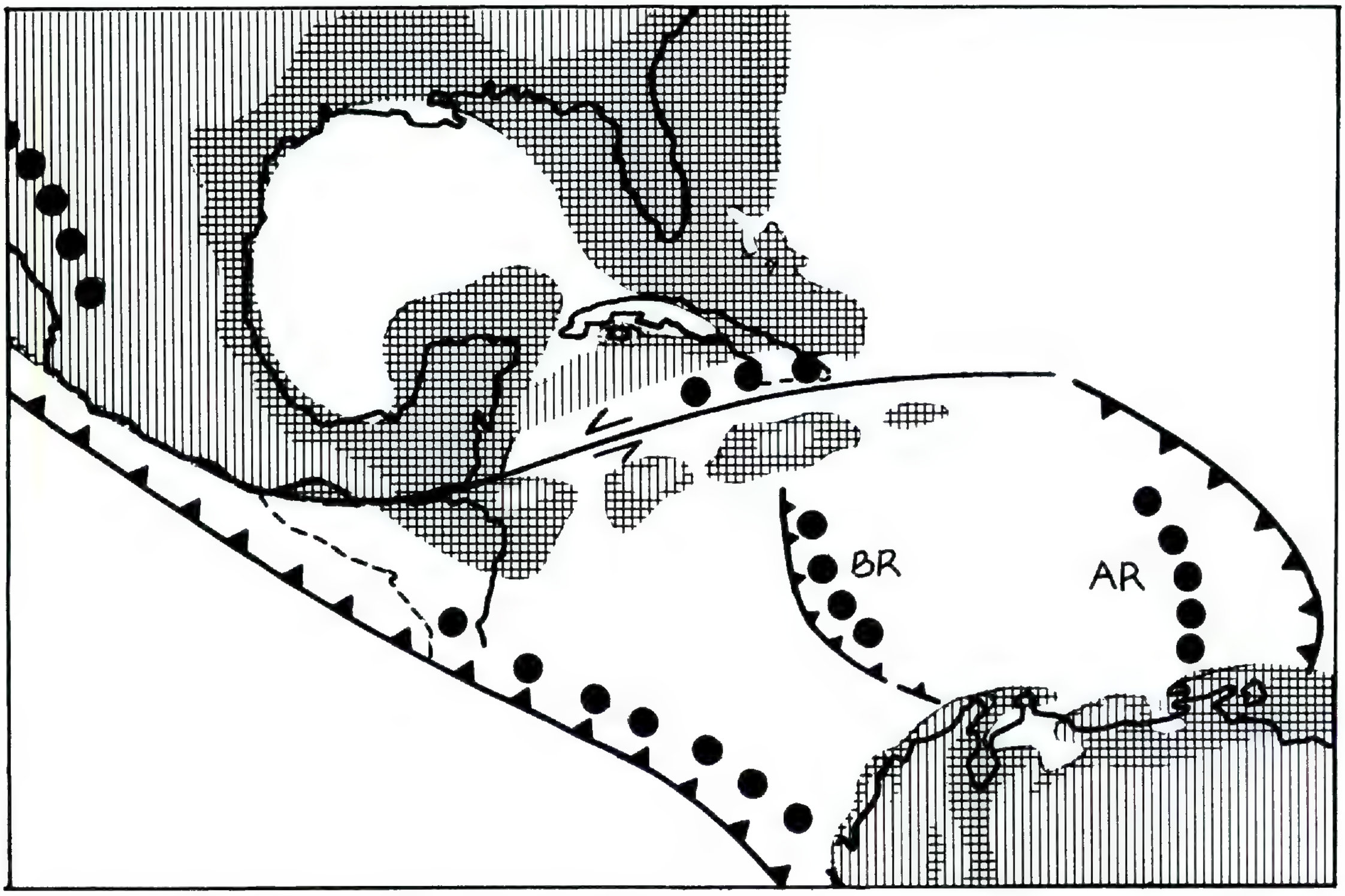


FIGURE 6. The Gulf of Mexico and the Caribbean region in the Paleocene (55 Ma) according to Salvador and Green (1980). The Beata and Aves Ridges (BR and AR respectively) are now emplaced and the Caribbean has undergone its maximum north–south expansion. A volcanic chain now extends between northwestern South America and the ultimate site of Honduras and Nicaragua.

ey's (1982) longitudinal displacement theory Honduras and Nicaragua (and by implication of polar position data, also Jamaica) had, along with Panama and Costa Rica, an older origin in the eastern Pacific and were emplaced as the proto-Caribbean/eastern Pacific sea floor was sucked into the Caribbean heartland. Thus, both kinds of theories include the potential for Antillean juxtaposition with northern Central America (Yucatan) at some time in their histories. The largest difference between them is how far east one should situate an island arc that joins northern Central America (Yucatan) with Colombia and in the ages and rates of motion of the Antillean components. But there seems little reason to argue that a single ancestral biota might have occupied large parts of what now are a series of isolated islands, thus providing major opportunities for biotic differentiation in a pattern of land connections and disconnections very much alike for both latitudinal and longitudinal displacement theories. From the standpoint of biogeography, then, the different theories disagree in some details and in focus, but agree in ways that concern biohistory.

HISTORICAL SUMMARY

150–165 MA

At this early stage North and South America were closely approximated, separated in what is now the Gulf region by the northern Central America (Yucatan) block, which later became the principal component of northern Central America (Yucatan). The Bahama platform lying due ESE of southeastern North America existed at this time. No elements of the Antilles would be recognizable at this period. Northern Central America (Yucatan), including southwestern Guatemala, Honduras, and Nicaragua, would, at this stage, be Pacific land (the Chortis block) lying to the southwest of what was to become Mexico. Africa, North America, and South America were all still in contact with a small piece of Africa lying athwart the southeastern segment of the already formed Appalachian chain and including Florida and the northern Bahamas. Major fault zones were beginning to form 1) to the north and south of northern Central America (Yucatan) in the Gulf region, 2) to the east, west, and south of the Bahama platform, the eastern part forming

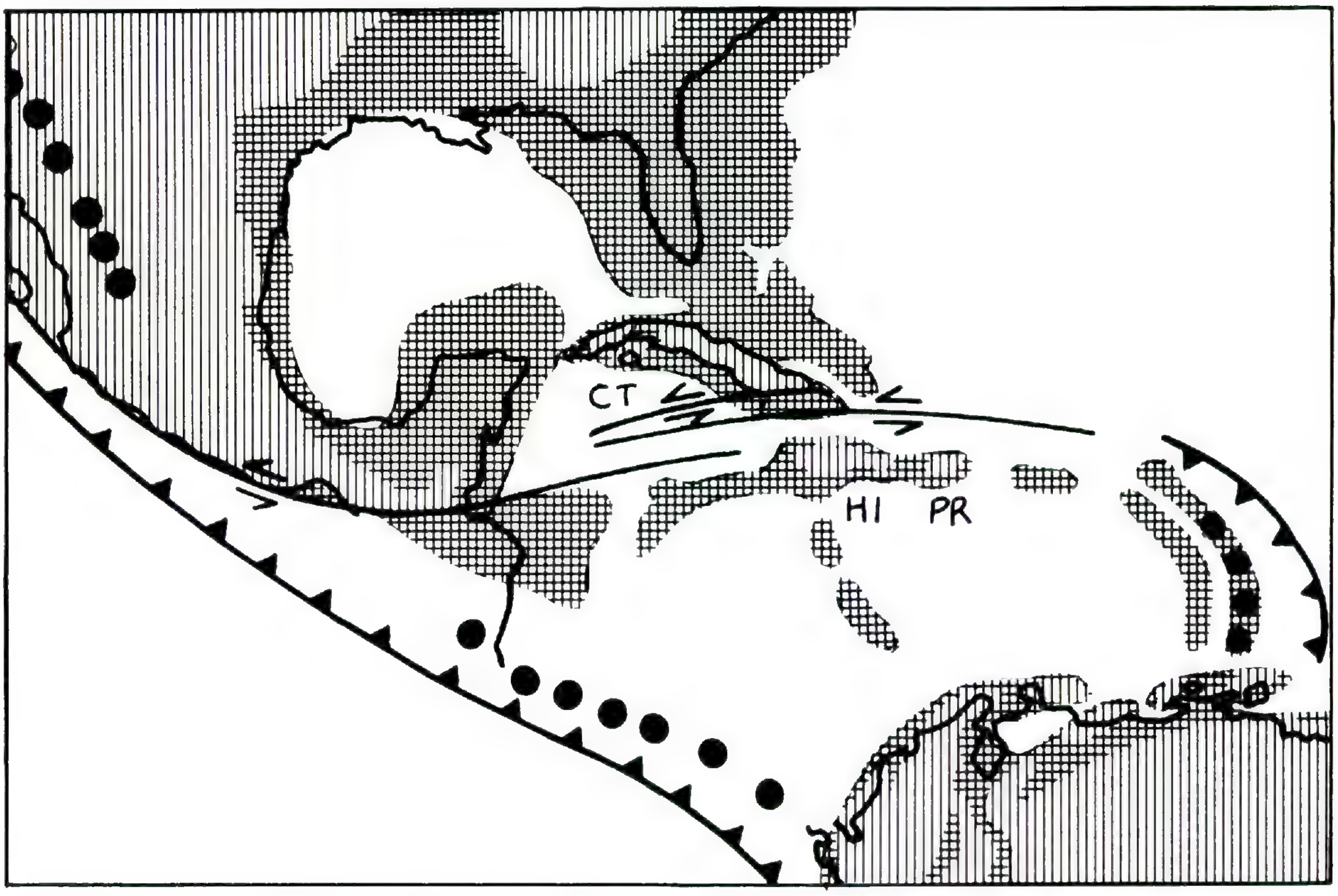
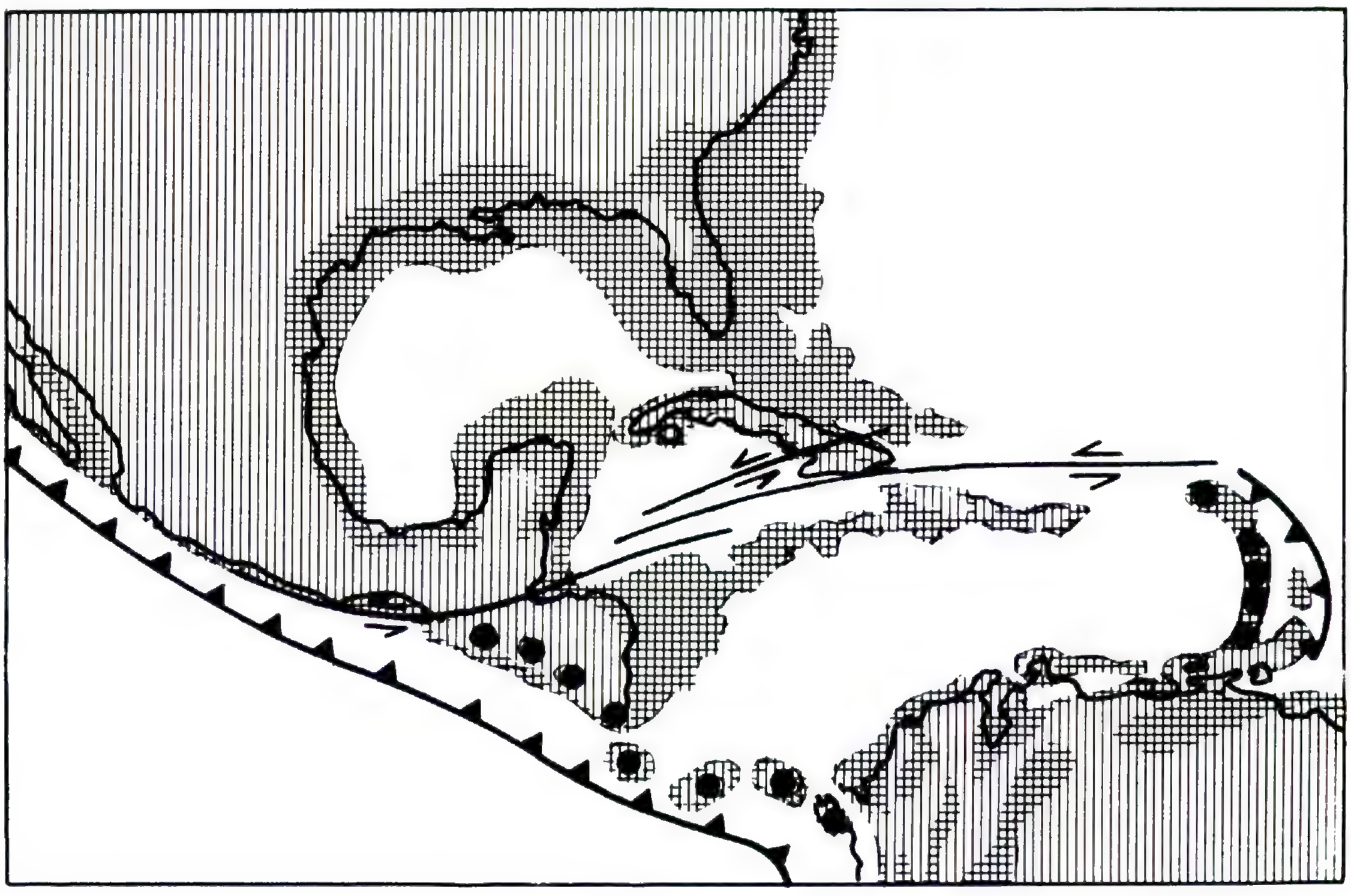


FIGURE 7. The Gulf of Mexico and the Caribbean region in the Middle Eocene (42 Ma) according to Salvador and Green (1980). A spreading center has now appeared in the Cayman Trough (CT), accentuating east–west translocation along the faults to the north and south of the Caribbean basin and the latter is being compressed by the motion of North and South America toward one another. In this model only Hispaniola (HI), Puerto Rico (PR), two sections of Cuba and the Isle of Pines are considered to be subaerial. The proto-Lesser Antilles have now appeared on the eastern border of the Aves Ridge.



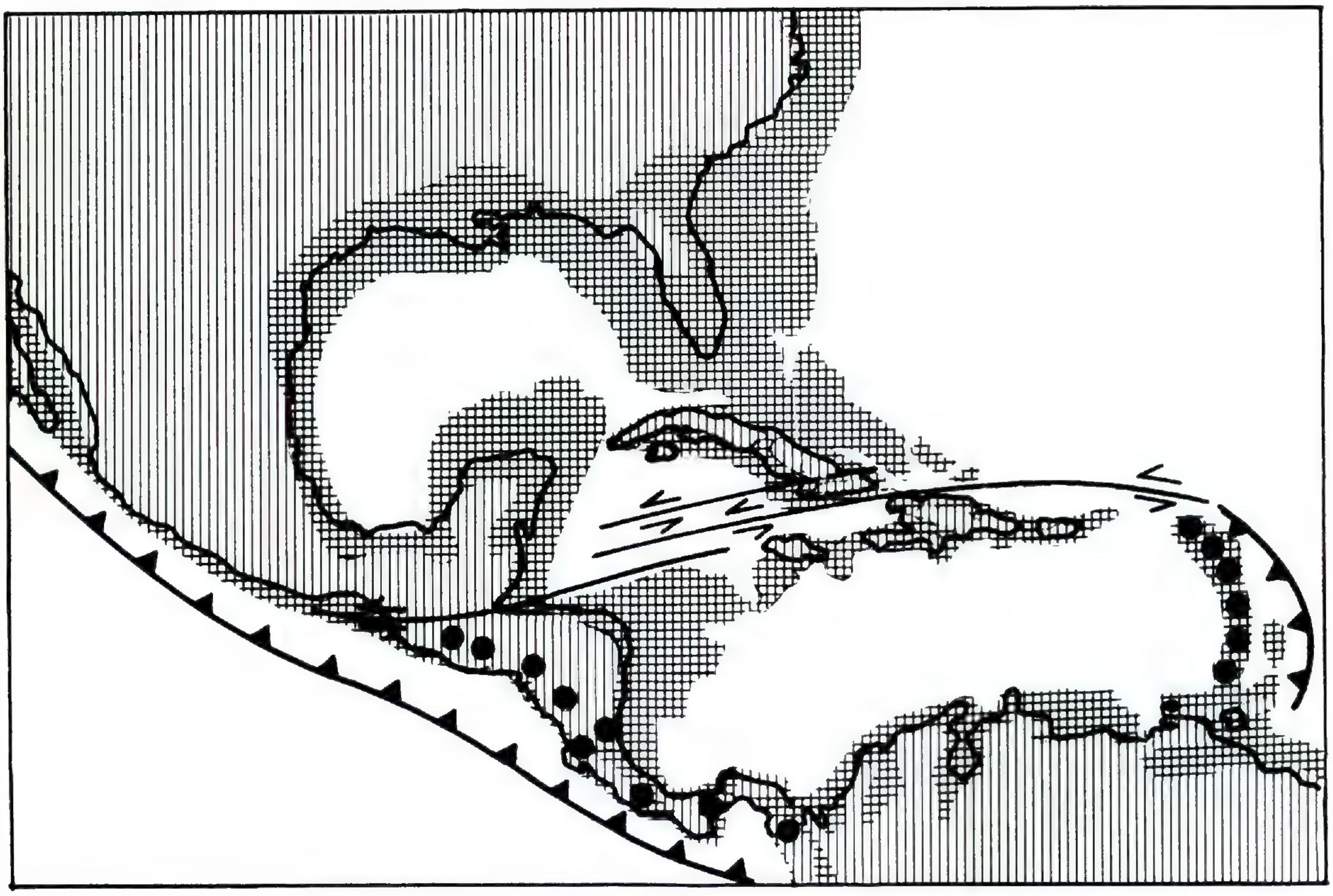


FIGURE 9. The Gulf of Mexico and the Caribbean region in the late Miocene (7 Ma) according to Salvador and Green (1980). The Caribbean basin has undergone nearly its maximum compression in relation to the Recent configuration, Cuba has consolidated into three sections, Hispaniola into two, and Jamaica and a major part of the Yucatan is subaerial.

a northern segment of the proto-mid-Atlantic ridge, 3) a southern segment of the proto-mid-Atlantic ridge between northeastern South America and the proto-Gulf of Guinea region of Africa, and 4) a major part of the western Central American Trench off the west coast of North America and South America.

95 MA

North and South America have now separated substantially, opening up the Gulf of Mexico and an area to the south that was later occupied by Caribbean sea floor. Northern Central America (Yucatan) has now become joined to Mexico, and the Chortis block has moved east to a position south of Mexico and west of northern Central America (Yucatan), the area of contact representing the origin of the Motagua-Polochic transform fault (= Cayman Trough). A proto-Antilles island arc, of volcanic origin, has formed between northern Central America (Yucatan) and western South America, and the Central American trench in this region has jumped to the east of the arc to form the leading edge of a subduction zone that will enable the proto-Antilles to override the proto-Caribbean sea floor. The western end of this island arc moved north, where; colliding with northern Central America (Yucatan); Jamaica, the Caymans, and southwestern Hispaniola were sheared off from western Cuba. Thus, Jamaica, the Caymans, southwestern Hispaniola, and western Cuba all accreted respectively to the southern and eastern parts of north-

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FIGURE 8. The Gulf of Mexico and the Caribbean region in the early Miocene (21 Ma) according to Salvador and Green (1980). North–south compression of the Caribbean basin continues. Lower Central America begins to emerge and undergo compressional deformation, Puerto Rico and three components of Hispaniola are present and subaerial, and Cuba and the Isle of Pines include seven separate subaerial components. Northern Central America (Honduras-Nicaragua) is now emplaced, having migrated eastward under the Yucatan (Nuclear Central America) along the Polochic-Motagua extension of the Cayman Trough.

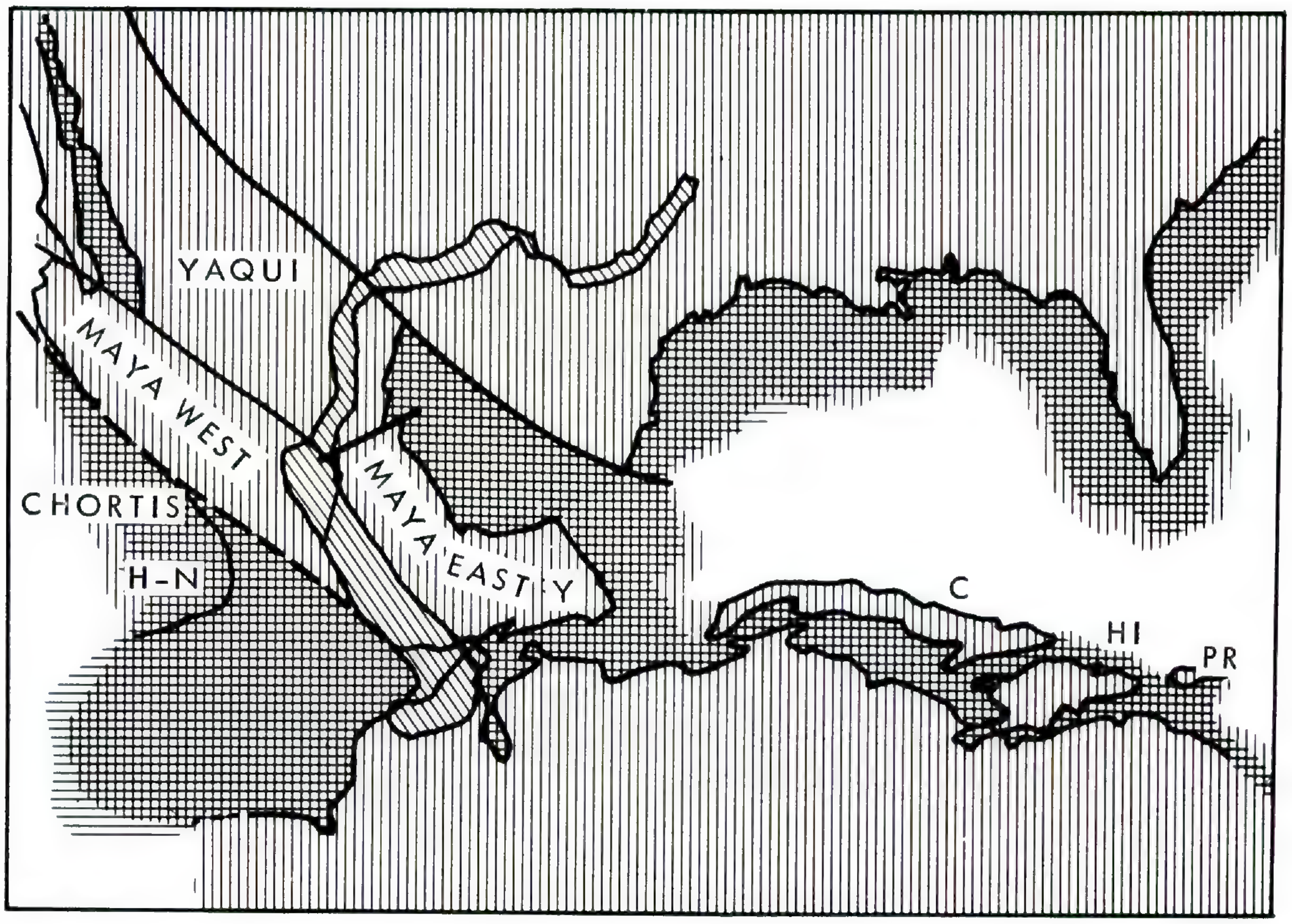

FIGURE 10. Post-Paleozoic to pre-Middle-Jurassic configuration of Middle America, the Gulf and Caribbean regions according to Anderson and Schmidt (1983). Vertical hatching is land, cross-hatching is shallow-water shelf, and oblique hatching is a reconstructed curvilinear belt of Paleozoic rocks that show lithologic and paleontologic similarities. The proposed positions of Yucatan (Y), Hispaniola (HI), and Puerto Rico (PR) are shown. This model also incorporates the notion that the region consisted of several microplates as labelled: Yaqui; Maya West; Maya East = Yucatan, in part; and Chortis = southern Guatemala, Honduras, and Nicaragua. Like the model of Salvador and Green (1980) this is a pre-Cenozoic description of the formation of the Gulf of Mexico and Caribbean by the north–south displacement of North and South America (see Figs. 11–17).

ern Central America (Yucatan). The attenuated Bahama platform made a southeastward approach to the northern South America trench, and the mid-Atlantic ridge is now well developed between Africa and North America, the former having left behind Florida and the small Appalachian segment mentioned above.

65 MA

North and South America have separated further along a modern north–south axis and the proto-Antillean arc had begun to stream eastward into the Caribbean heartland opened up by the separation of North and South America. The Oriente of Cuba is now situated to the east, contacting the Bahama platform along its northeastern margin and nuclear Hispaniola to the south. Southwestern Hispaniola, the Caymans, and Jamaica have begun an eastward migration away from the southern edge of northern Central America (Yucatan), moving along the proto-Cayman trough, which has a complex structure including pieces to the north, west, and south of Cuba and a north–south arm southeast of the Bahama platform that is to become the leading eastern edge of the Caribbean plate. The Aves Ridge or proto-Lesser Antilles has formed just behind this leading plate margin. The Chortis block has also begun a southeastward migration along the Motagua-Polochic fault, carrying it closer to northern Central America (Yucatan),

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FIGURE 12. The Gulf of Mexico and Caribbean region in the Middle Jurassic (150 Ma) according to Anderson and Schmidt (1983). As a result of latitudinal displacement of North and South America the proto-Greater Antilles are depicted as moving north away from South America.

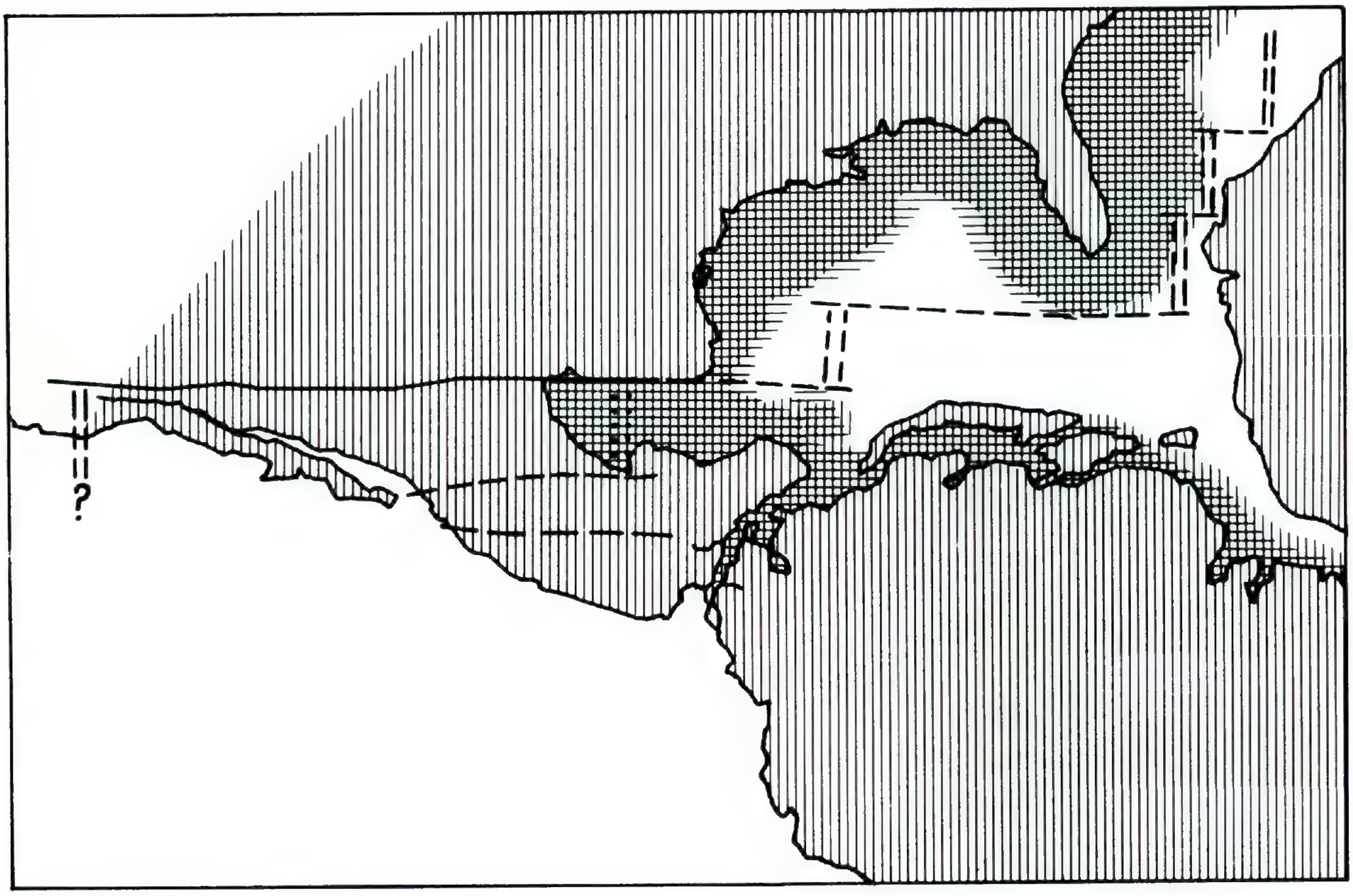
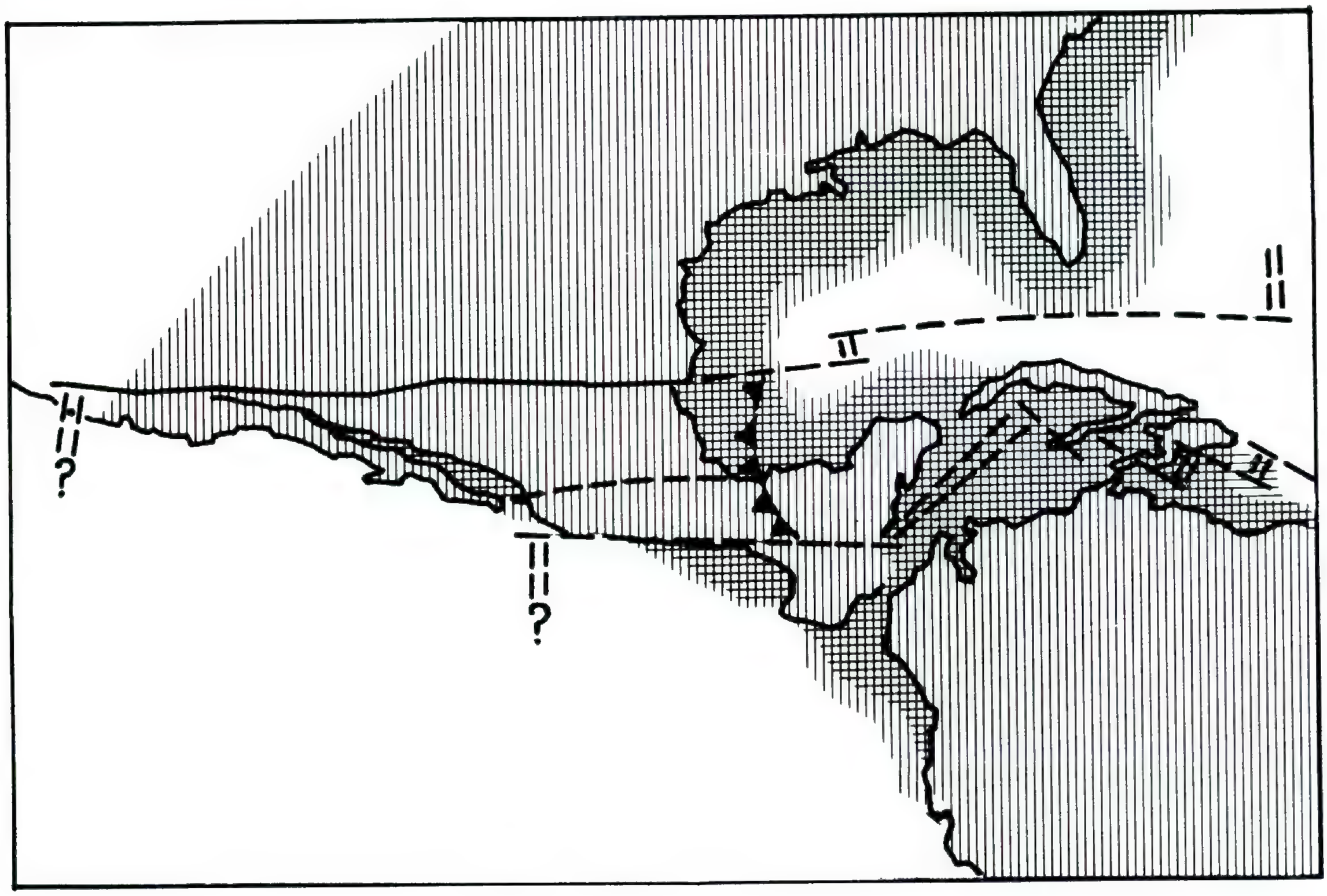


FIGURE 11. The Gulf of Mexico and Caribbean region in the Middle Jurassic (160 Ma) according to Anderson and Schmidt (1983). The proto-mid-Atlantic ridge can be seen between south-eastern North America and north-western Africa as a three-step inferred fault of broken lines. Vertical hatching is land, cross-hatching is shallow-water shelf, unbroken heavy lines is the original position of the Mojave-Sonora megashear that bounds the Yaqui microplate to the north (see Fig. 10), broken heavy lines are inferred faults.



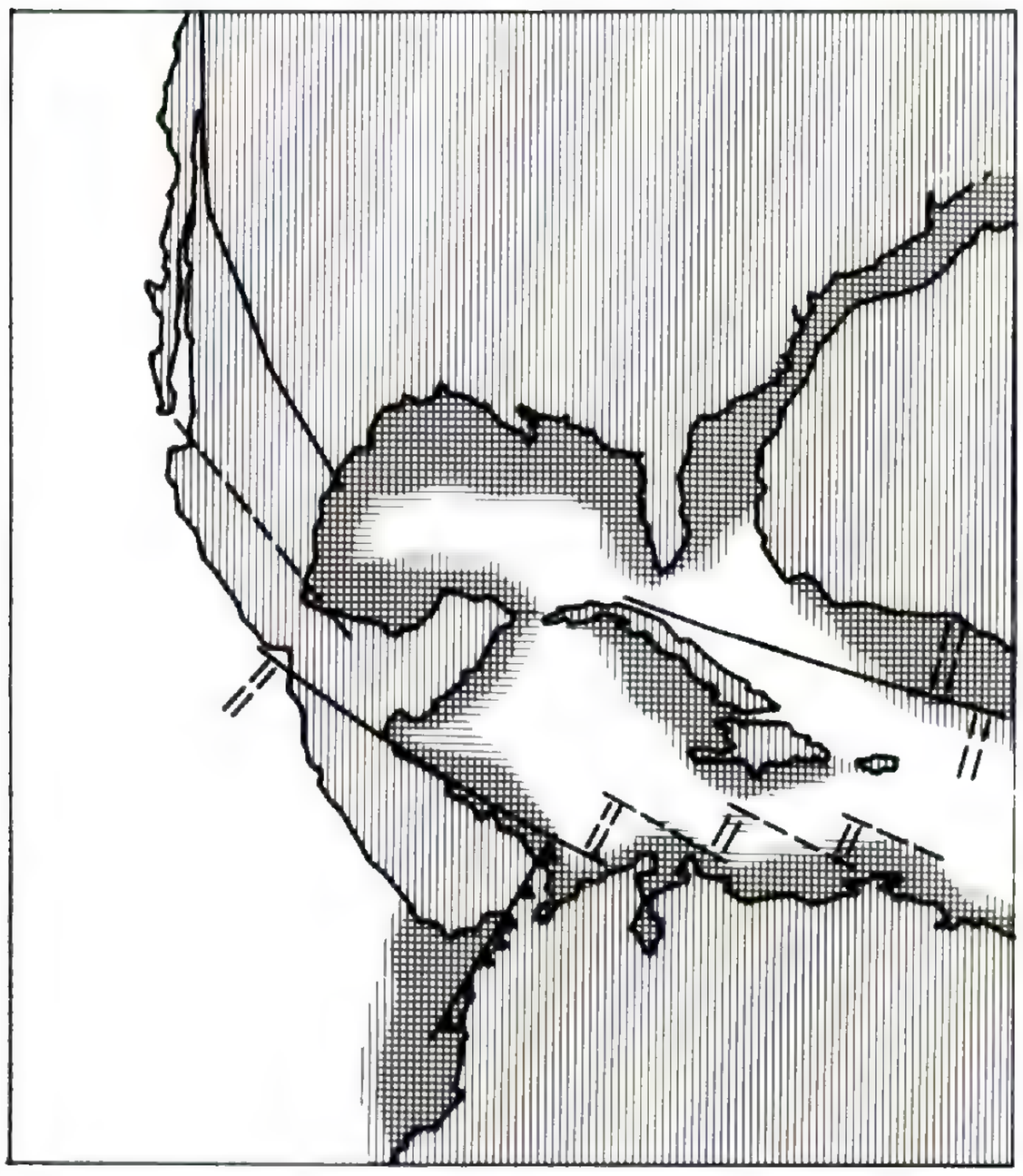


FIGURE 13. The Gulf of Mexico and Caribbean region in the Kimmeridgian (ca. 140 Ma) according to Anderson and Schmidt (1983). Compare with Figure 1.

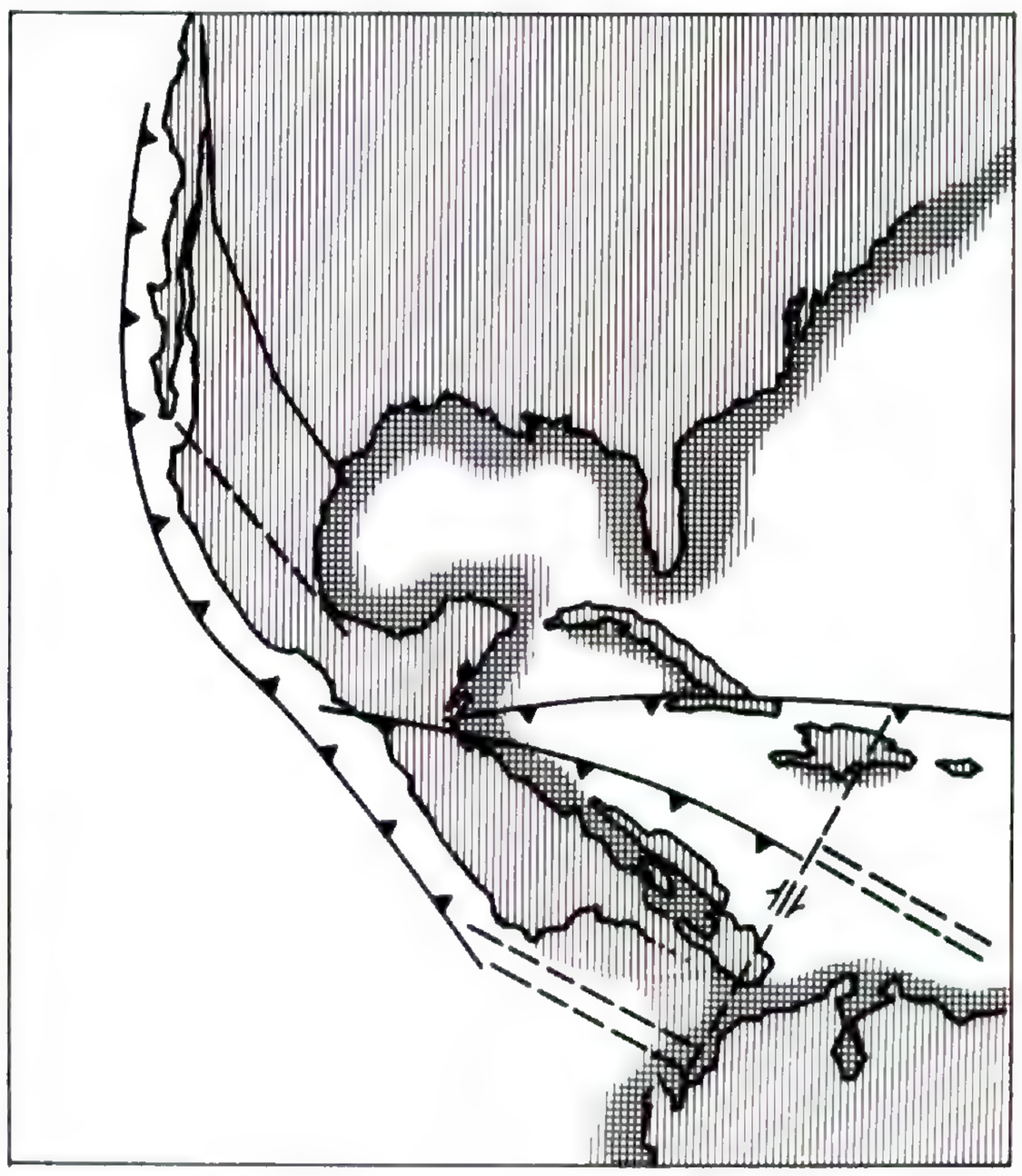


FIGURE 15. The Gulf of Mexico and Caribbean region in the latest Cretaceous (ca. 70 Ma) according to Anderson and Schmidt (1983). Latitudinal displacement is still continuing.

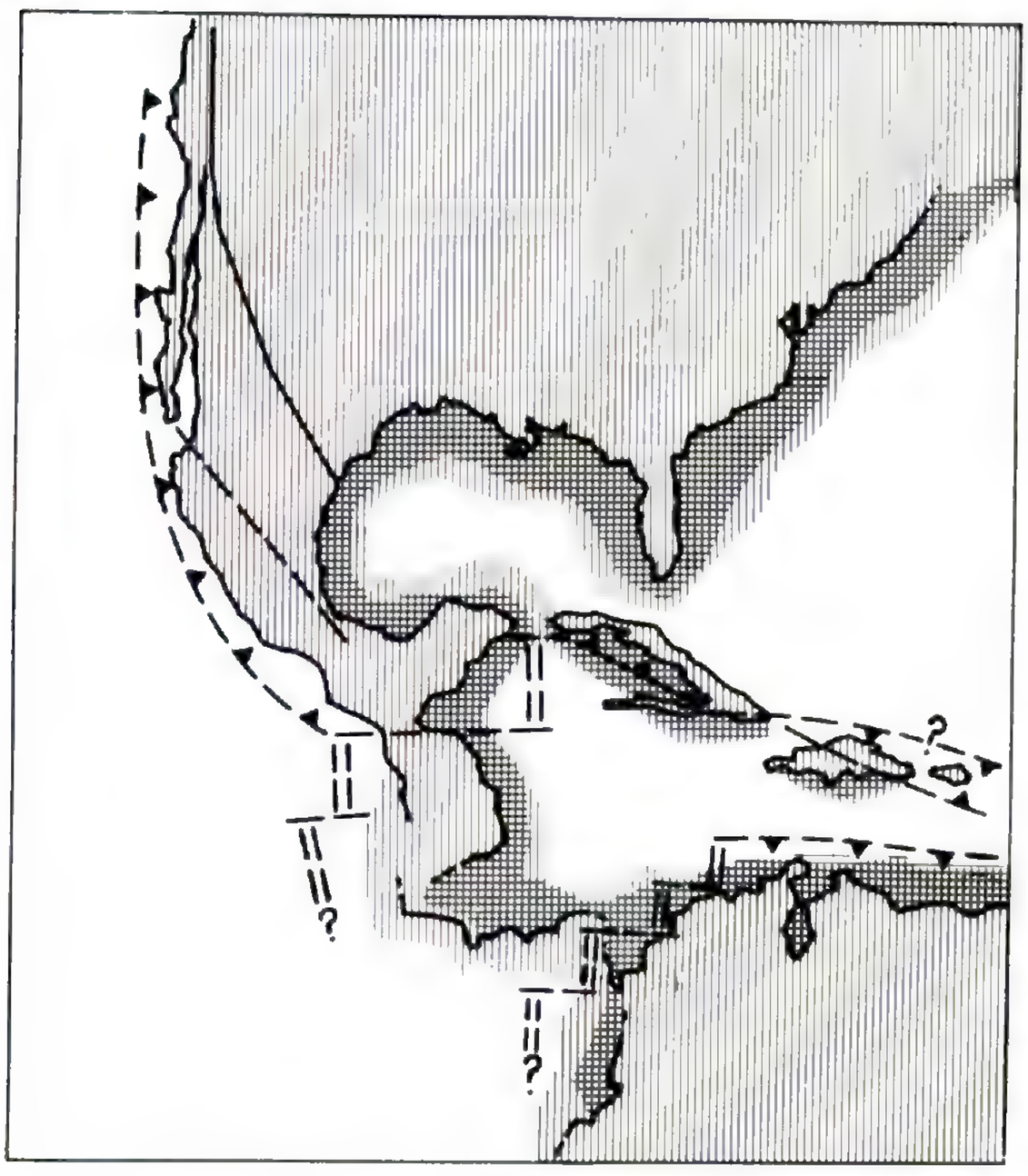


FIGURE 14. The Gulf of Mexico and the Caribbean region in the Late Cretaceous (ca. 95 Ma) according to Anderson and Schmidt (1983). In this reconstruction western Cuba has just made contact with the Yucatan and Bahama platforms. Compare with Figure 4.

and lower Central America has moved in from the eastern Pacific to suture with the Chortis block.

PRESENT TO 9 MA

During this pre-modern epoch in Caribbean history nuclear Hispaniola continued its eastward movement, separating from the Oriente of Cuba and being joined by southwestern Hispaniola (about 9 Ma) and picking up a small southern piece of the Bahama platform along its northern edge (about 3 Ma). Jamaica and the Caymans have trailed behind maintaining a steady distance from southwestern Hispaniola, so that, although at one time connected by contiguous land to Cuba and Hispaniola through northern Central America (Yucatan), the former islands have been isolated fragments for most of Caribbean geohistory (during which, the White Limestone Group of central Jamaica was continuously subaerial, Robinson, 1976; Robinson et al., 1977). Central America now occupies the site, formerly the province of the proto-Greater Antilles, and is joined to the precursor lands of western Colombia (the area of the Rio Cauca and Magdalena basins). The Cayman Trough has a complex configuration including a spreading center between its northern and southern slip-fault components.

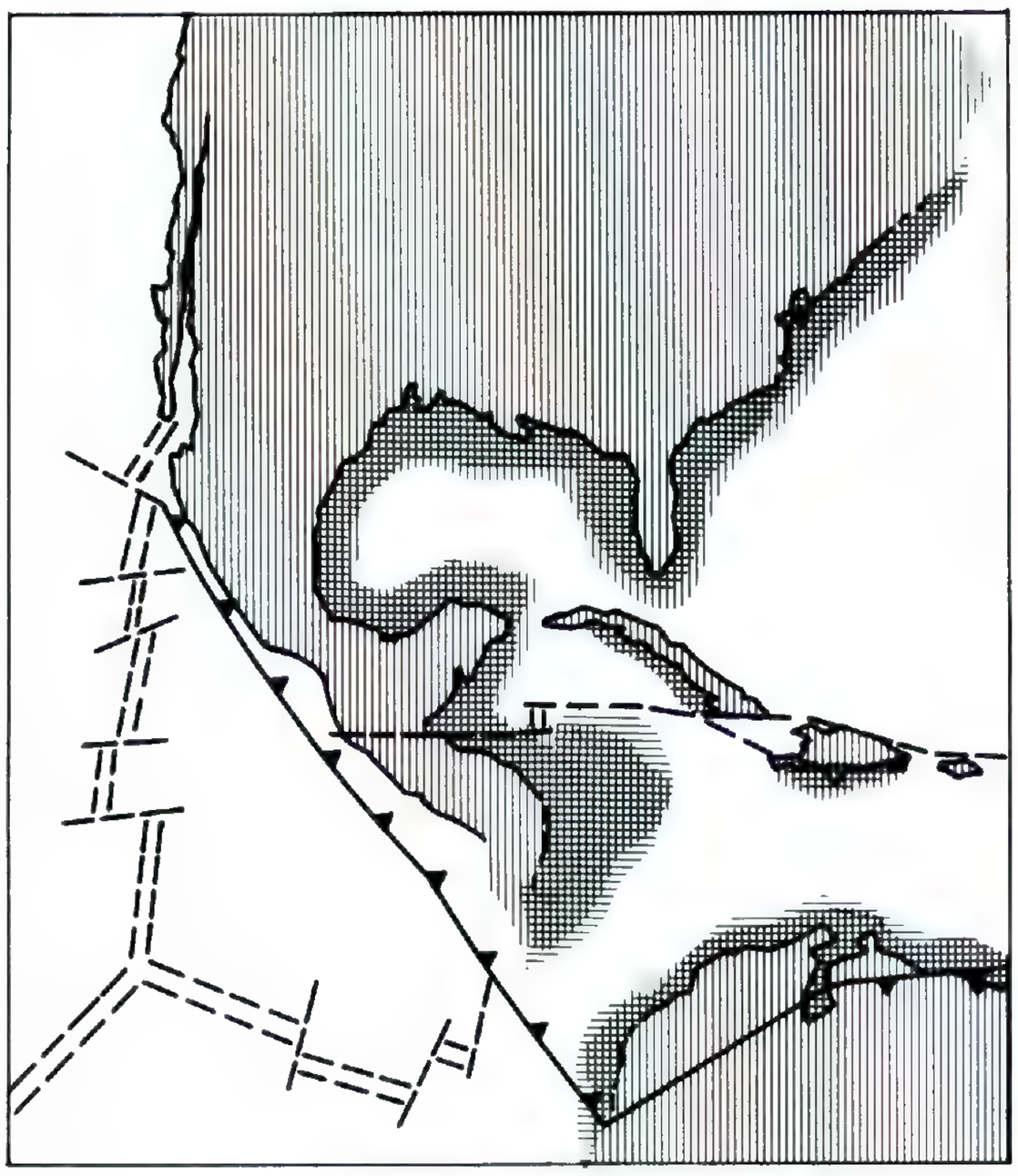


FIGURE 16. The Gulf of Mexico and the Caribbean region in the Miocene (ca. 8 Ma) according to Anderson and Schmidt (1983). Compare with Figures 8 and 9. Latitudinal expansion has ceased and northern Central America (Honduras and Nicaragua) remain isolated from northwestern South America.

The southern component is now continuous with the active Motagua-Polochic left-lateral transform fault, which connects with the again unbroken western Central Americas Trench. The northern component of the major Antillean trench system continues eastward between the Bahama platform and the formerly Bahamian section of northern Hispaniola and ultimately

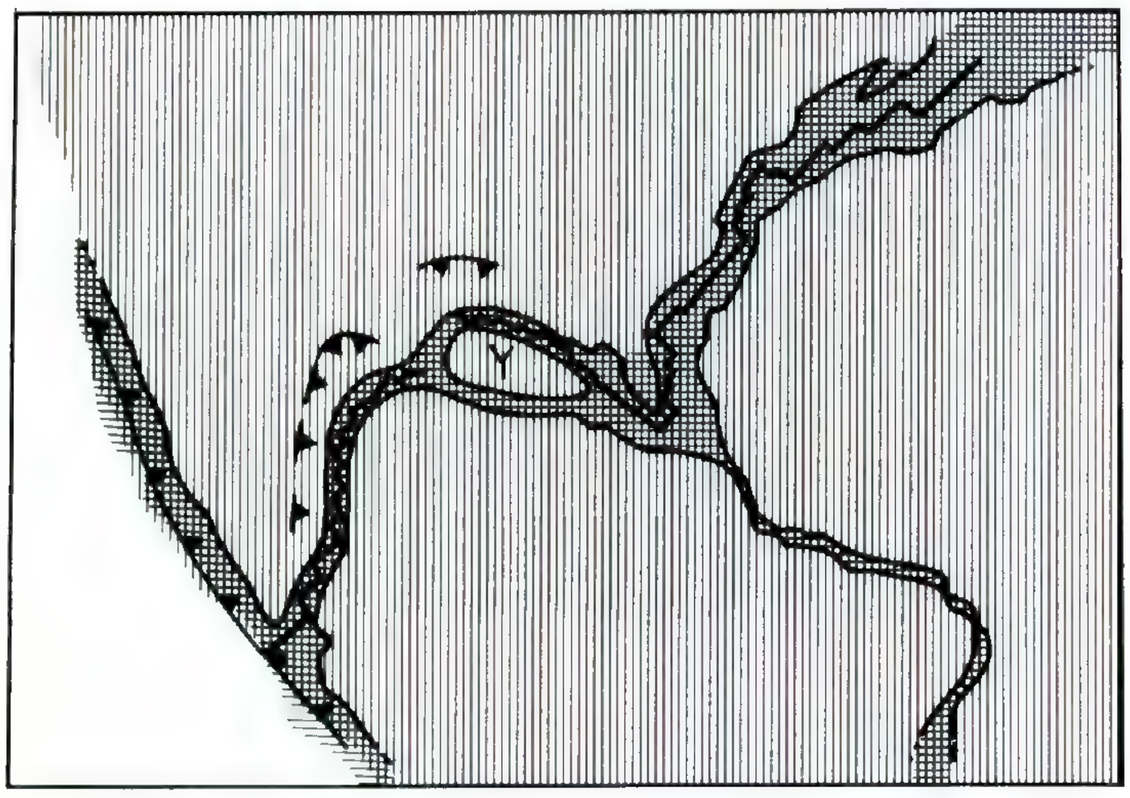


FIGURE 17. The Gulf of Mexico and the Caribbean region in late Pangaean time (ca. 165 Ma) according to Pindell and Dewey (1982). Yucatan (Northern Central America, Y) is depicted here as a separate microplate between North and South America.

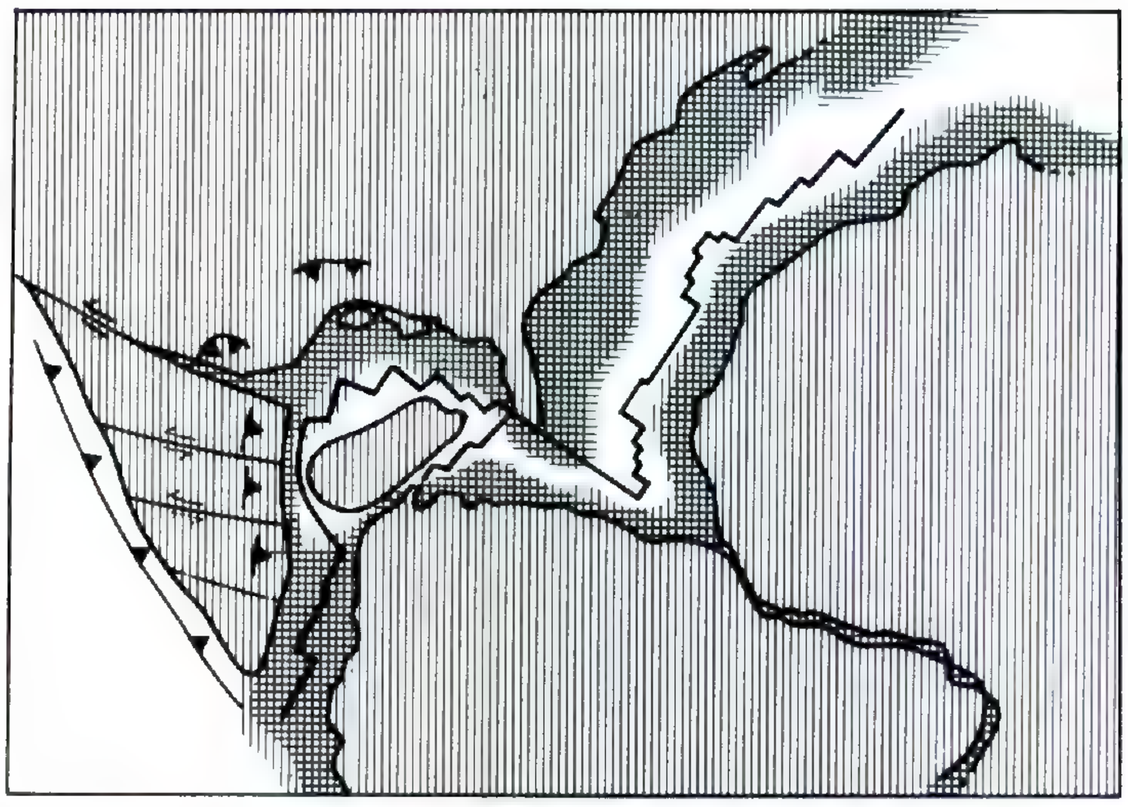


FIGURE 18. The Gulf of Mexico and the Caribbean region prior to the separation of Africa and South America (ca. 150 Ma) according to Pindell and Dewey (1982). The heavy east–west lines across Mexico are areas of thrusting that separate Mexico from southwestern North America at roughly the level of the Rio Grande and that subdivide Mexico into four discrete zones.

connects with the subduction zone along the leading eastern edge of the Caribbean plate behind which the modern Lesser Antilles have emerged as chains of volcanic stepping-stones from the precursor Aves Ridge. With the ultimate disappearance of the Cauca-Magdalena, transgressing seaway in northwestern Colombia, a new continuous land connection was made between North and South America.

HISTORICAL SUMMARY

To the extent that the foregoing account is correct, one can say that the Caribbean land and

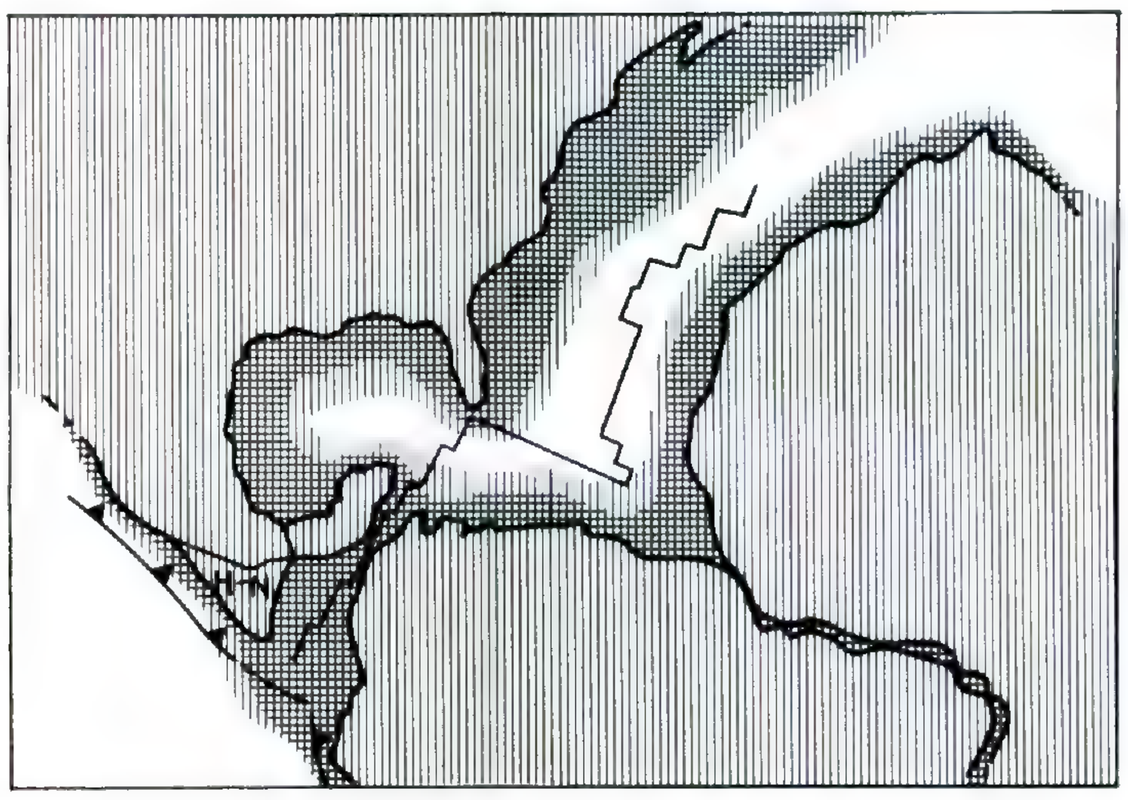


FIGURE 19. The Gulf of Mexico and Caribbean region in the Kimmeridgian (140 Ma) according to Pindell and Dewey (1982). The Yucatan block has rotated into position and been sutured to southern Mexico. Northern Central America (Honduras and Nicaragua, H-N) is depicted as already sutured to southwestern Mexico.

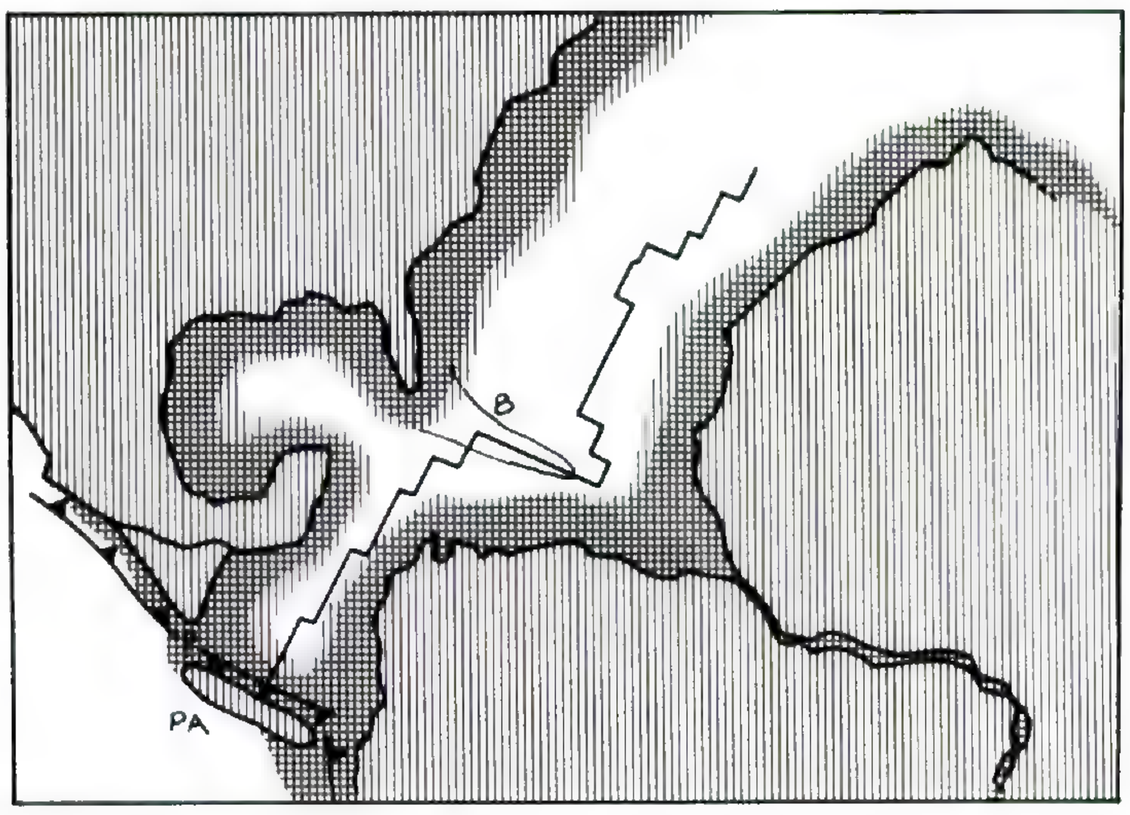


FIGURE 20. The Gulf of Mexico and Caribbean region at the time of formation of a proto-Antillean archipelago (PA) at 125 Ma, according to Pindell and Dewey (1982). The Bahama platform (B) can be seen extending in an ESE direction toward the proto-mid-Atlantic ridge.

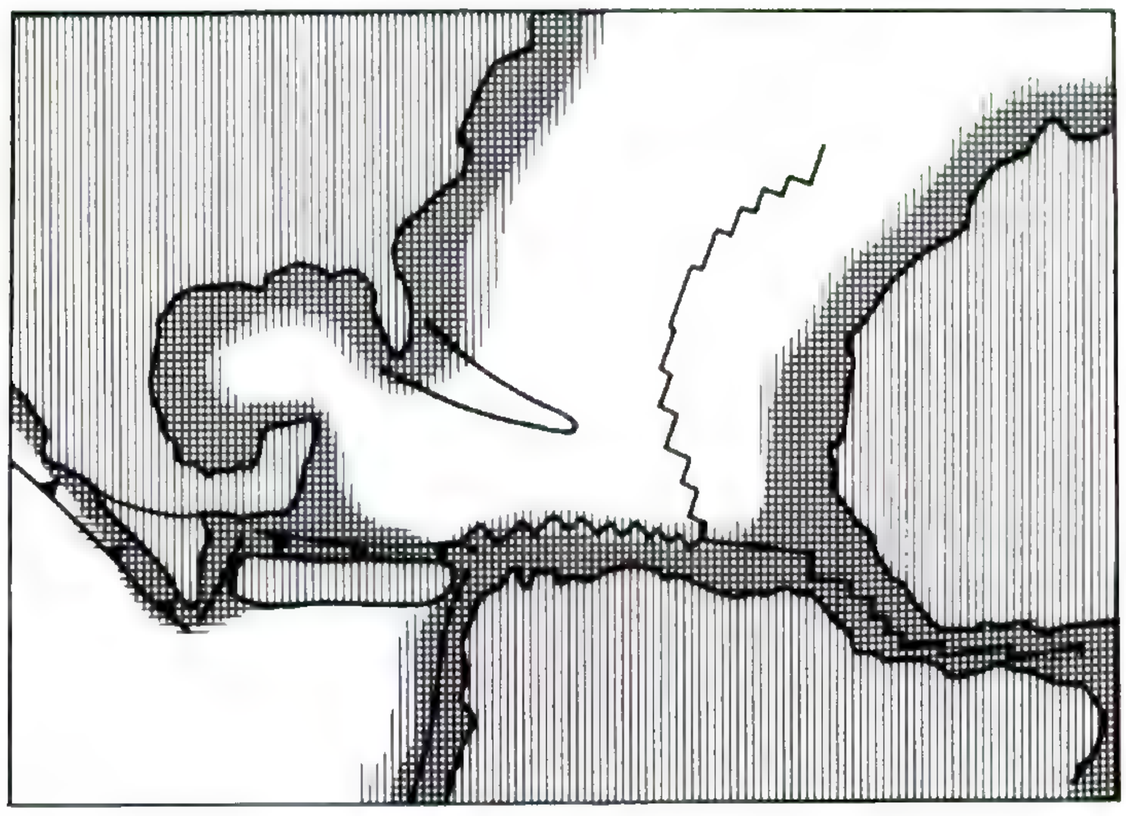


FIGURE 22. The Gulf of Mexico and the Caribbean region as eastern Pacific seafloor is initially being sucked into the Caribbean region at about 95 Ma, according to Pindell and Dewey (1982).

water had a complex history of connections between different geographic features being made and then broken and then reformed in another configuration. The history includes eight events of fragmentation and seven of hybridization. This is summarized below in the series of included maps that show that vicariant opportunities for the biota are about as numerous as hybridization events that provide opportunities for mixing of biotas. The geology of Hispaniola provides perhaps the most dramatic example of these two aspects of geohistory since it is alleged to have had a history of prior connection with northern Central America (Yucatan), Cuba, Jamaica, the Bahamas and an early process of fragmentation from other proto-Antillean components into major segments that behaved independently for most of their reconstructed history. But perhaps the most interesting part of Caribbean geohistory is that involving the Chortis block and lower Central America, which appear to have been Pacific land accreted into the eastern margin of the Pacific borderlands, thus recalling some elements of the Pacifica concept of Nur and Ben-Avraham (1977). Another recent study has further documented the incorporation of allochthonous terranes into western North America (Minckley et al., in press). If part of the same phenomenon,

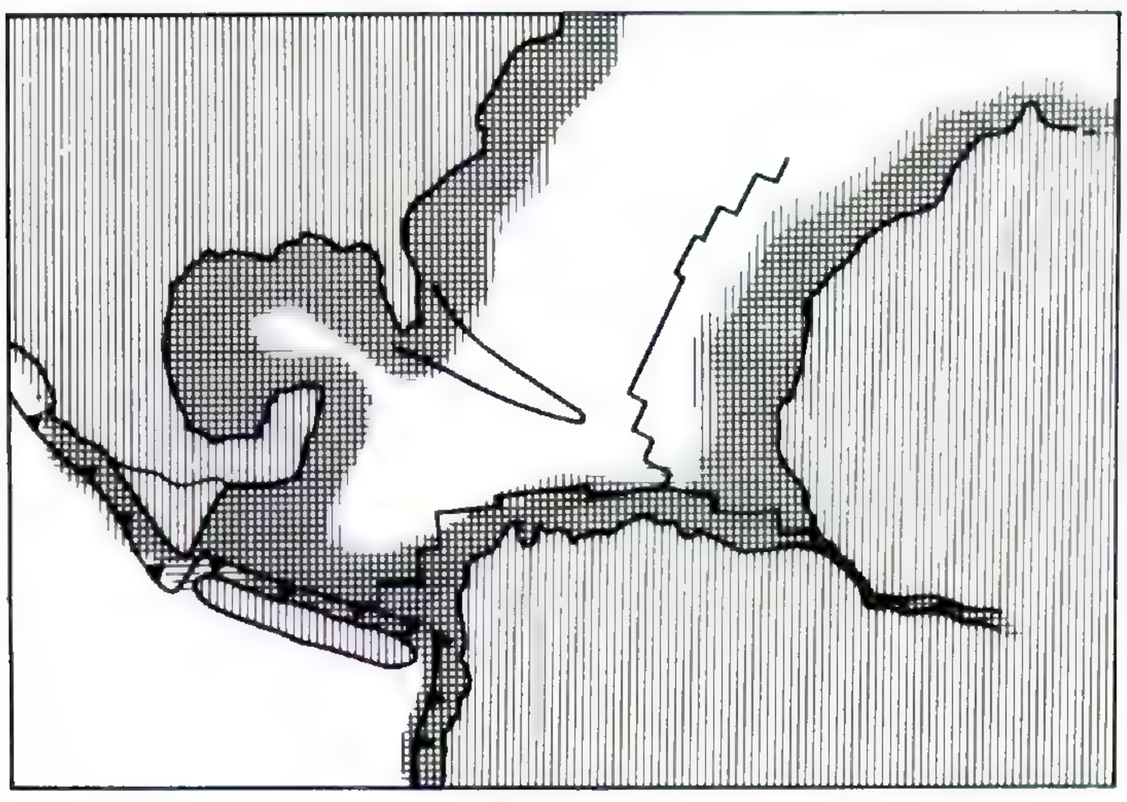


FIGURE 21. The Gulf of Mexico and the Caribbean region at the onset of separation of Africa and South America at 110 Ma, according to Pindell and Dewey (1982). The proto-Antillean archipelago has already moved slightly to the east of its position in the preceding figure.

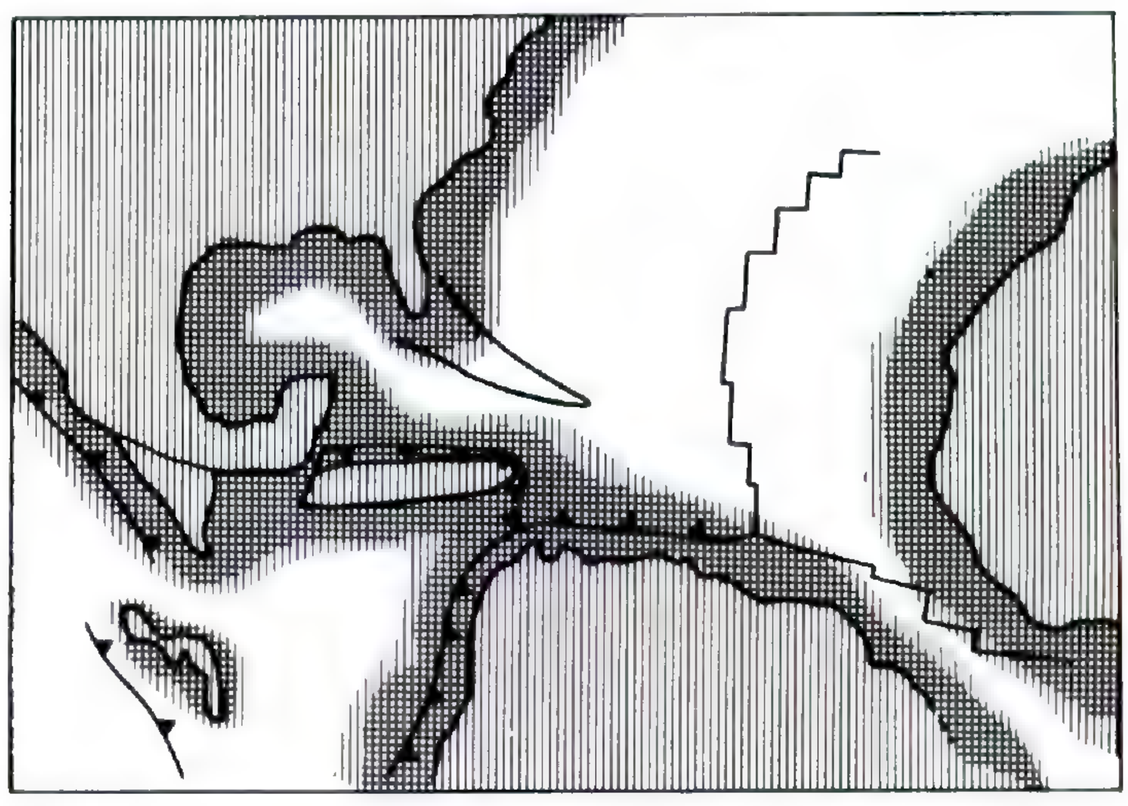


FIGURE 23. The Gulf of Mexico and the Caribbean region as the proto-Antillean archipelago at 80 Ma, according to Pindell and Dewey (1982), moves ENE toward the Bahama platform and a contact with the southeastern margin of the Yucatan. Note also the reconstruction of lower Central America as an eastern Pacific island arc near the western boundary of the Caribbean plate.

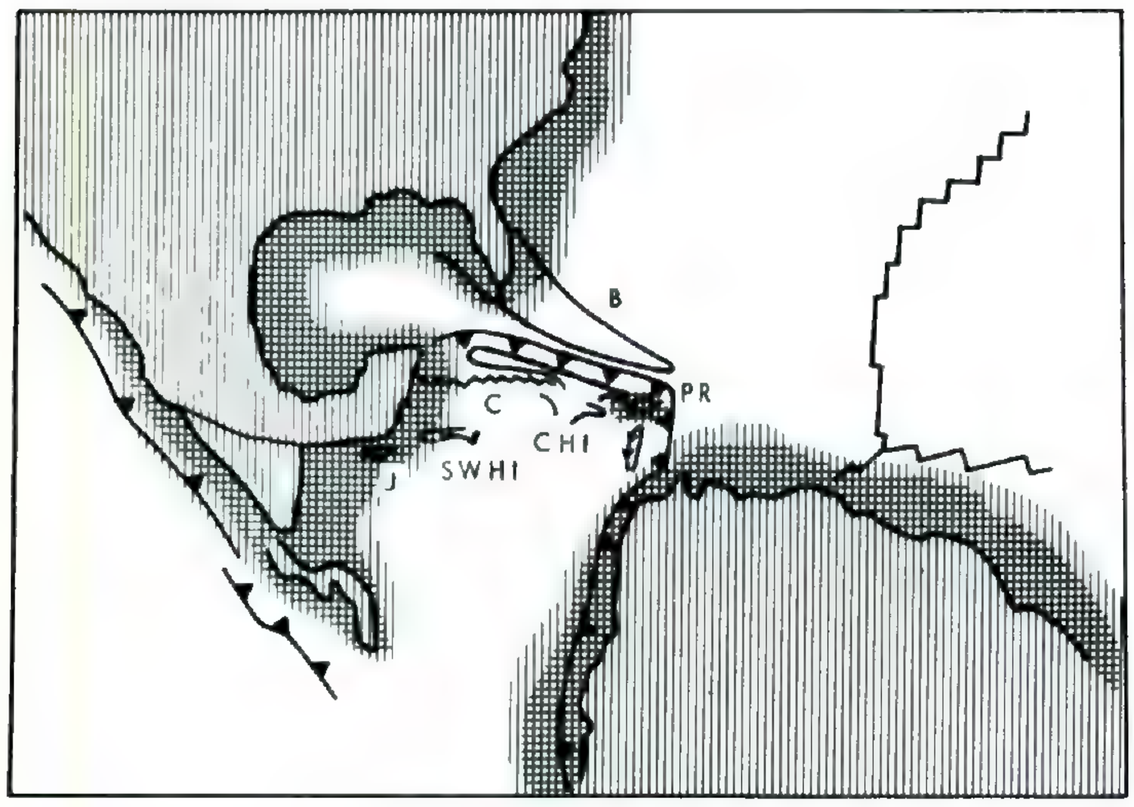


FIGURE 24. The Gulf of Mexico and the Caribbean region as the proto-Antillean archipelago begins to differentiate into recognizable components of the Greater Antilles at 65 Ma according to Pindell and Dewey (1982): Jamaica (J), central Hispaniola (SWHI), Puerto Rico (PR), and Cuba (C) that lies just north of the beginnings of the Cayman Trough (jagged line and CHI).

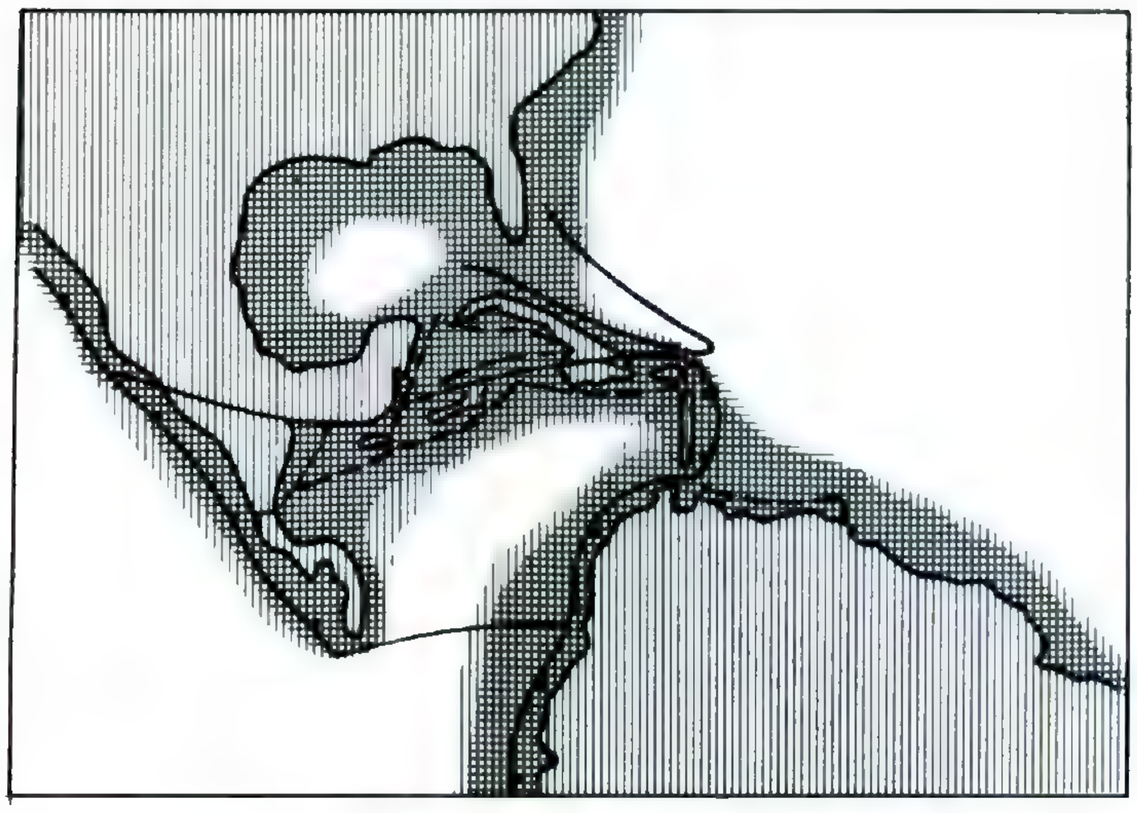


FIGURE 26. The Gulf of Mexico and the Caribbean region at about 36 Ma when many of the Antillean elements have been differentiated, the Cayman Trough has become active and northern Central America has begun its eastward motion along the Polochic-Motagua fault, and central Hispaniola is sutured to southwestern Cuba according to Pindell and Dewey (1982).

the history of Central America might well be shared with that of the exotic terranes along the western margins of North and South America, including perhaps the Carnegie Ridge system (the Galapagos and Cocos Islands) (see Rosen, 1976).

DERIVING GEOLOGICAL AREA CLADOGRAMS

With a history this complex it must be obvious that no simple branching diagram can exactly express all the implied relationships nor, because of hybridizations, is a completely resolved branching diagram possible. It is, therefore, my conclusion that most profit is to be gained from isolating parts of Caribbean history that represent stages in the evolution of land and water and therefore stages during which today's complex biota can be understood. There is evidence from occurrences of endemic species that some major monophyletic groups have been around for a very long time, e.g., gars, synbranchid eels, land iguanas, decapod crustaceans, and probably also cichlid fishes (see Rosen, 1976). Regarding the West Indian butterfly fauna, Brown (1978) has written: "It is possible that the original fauna

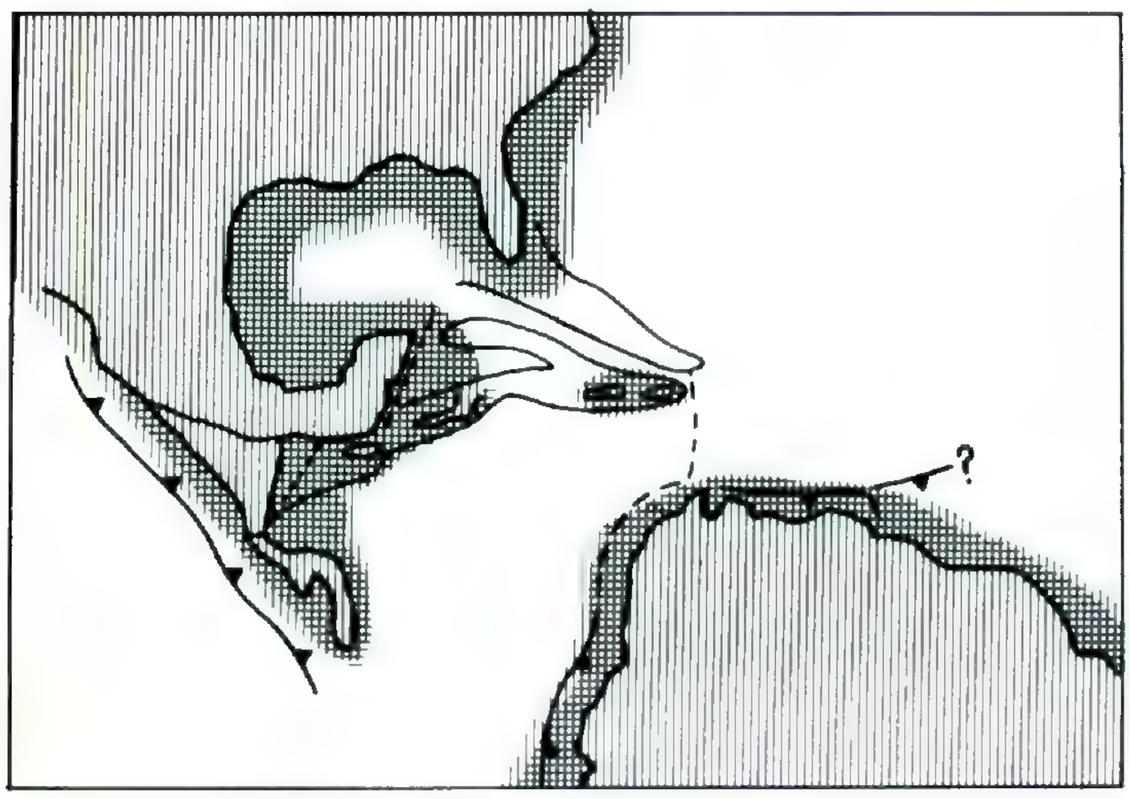


FIGURE 25. The Gulf of Mexico and the Caribbean region showing further differentiation of the Greater Antilles, the approximation of Cuba with the Bahama platform, and the suturing of lower Central America onto northern Central America at about 53 Ma according to Pindell and Dewey (1982).

FIGURE 27. The Gulf of Mexico and the Caribbean region at about 21 Ma when, according to Pindell and Dewey (1982), a spreading center has appeared in the Cayman Trough thus speeding the eastward movement of Jamaica, southwestern Hispaniola, and the disjunction of central Hispaniola and Cuba.

FIGURE 28. The Gulf of Mexico and the Caribbean region at about 10 Ma when, according to Pindell and Dewey (1982), Central America has made its closest approach to northwestern South America, Hispaniola is nearly assembled into its modern configuration and is almost disjunct from Cuba while making its closest approach to the southwestern tip of the Bahama platform.

FIGURE 29. The Gulf of Mexico and present plate boundaries and land areas in the Caribbean region from Pindell and Dewey (1982).

of the region had its roots in Africa at the close of the Mesozoic Era. Very little of this fauna is left but there are some indications of it." Other taxa seem to reflect events in the less remote periods of North and Middle American biohistory (Rosen, 1978). It would, therefore, be most helpful to be able to compare biological area cladograms with specific periods in geohistory rather than, as was done before (Rosen, 1976), to simply identify components the modern biota that are consilient with some features of today's complex geography. Thus one must introduce a

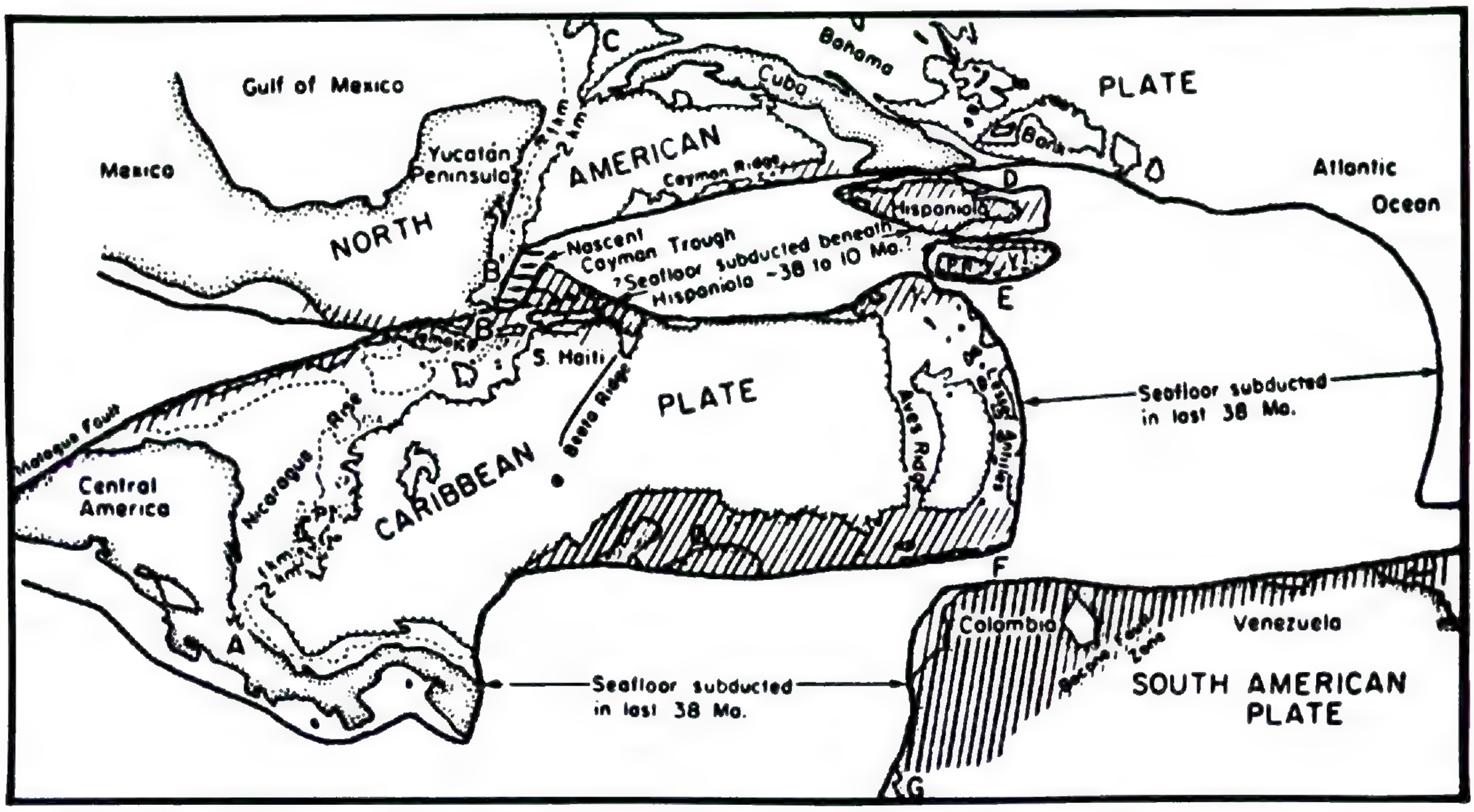
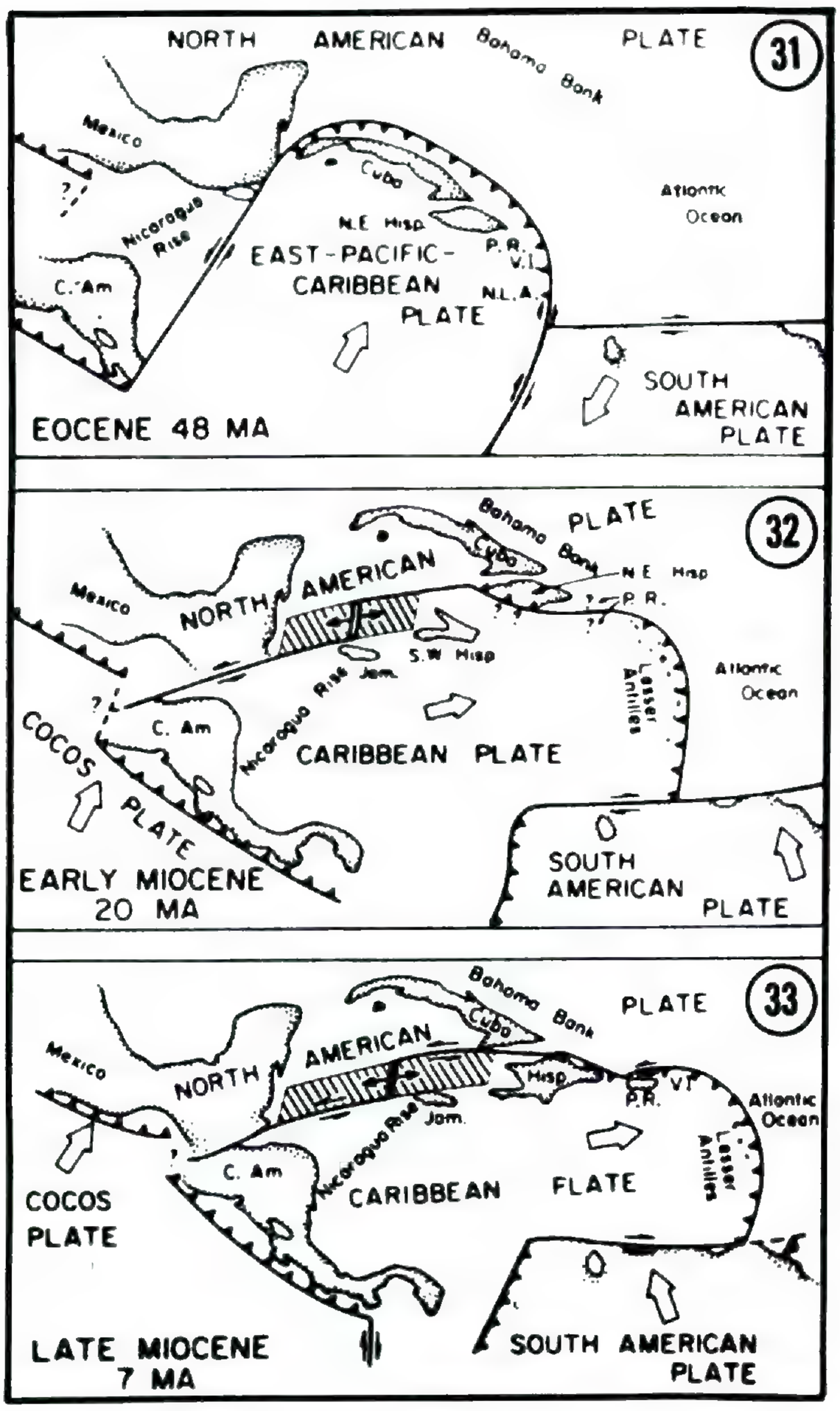


FIGURE 30. Caribbean microplate boundaries during the late Eocene (ca. 38 Ma) according to Sykes et al. (1982). In earlier Eocene times (ca. 48 Ma) Cuba, Hispaniola, and Jamaica are depicted as an archipelago extending from Yucatan toward northwestern South America (Fig. 31). In this reconstruction Puerto Rico is a neomorphic crustal feature that became subaerial late in Cenozoic history, but originally lay just south of the central Hispaniolan microplate and as in the Pindell and Dewey (1982) model. Hispaniola is complex incorporating a separate southwestern component and a small piece of the Bahamas to the north. Note that most of the main Antillean elements have, at most, a mid-Cenozoic age and that lower Central America was associated with the Chortis block by the early Miocene prior to an isthmian connection between North and South America.



FIGURES 31–33.—31. The eastern Pacific and Caribbean in mid-Eocene times (ca. 48 Ma) according to Sykes et al. (1982). An intimate association between Jamaica, Cuba, and Hispaniola is depicted.—32. The Caribbean plate in early Miocene times (ca. 20 Ma), according to Sykes et al. (1982), showing the formation of a Cayman Trench spreading center on the site of the older Cayman Ridge, the continued association of central Hispaniola with eastern Cuba, and a now completed Chortis block/Isthmian Bridge.—33. The Caribbean in nearly its modern configuration in late Miocene times (ca. 7 Ma), according to Sykes et al. (1982), showing the still unconnected Isthmian Bridge with northwestern South America and the movement of Cuba eastward away from Yucatan. The Eocene age of this depiction is consistent with the age determinations of Wadge and Burke (1983) who also estimate a rate of plate motion of about 4 cm per year.

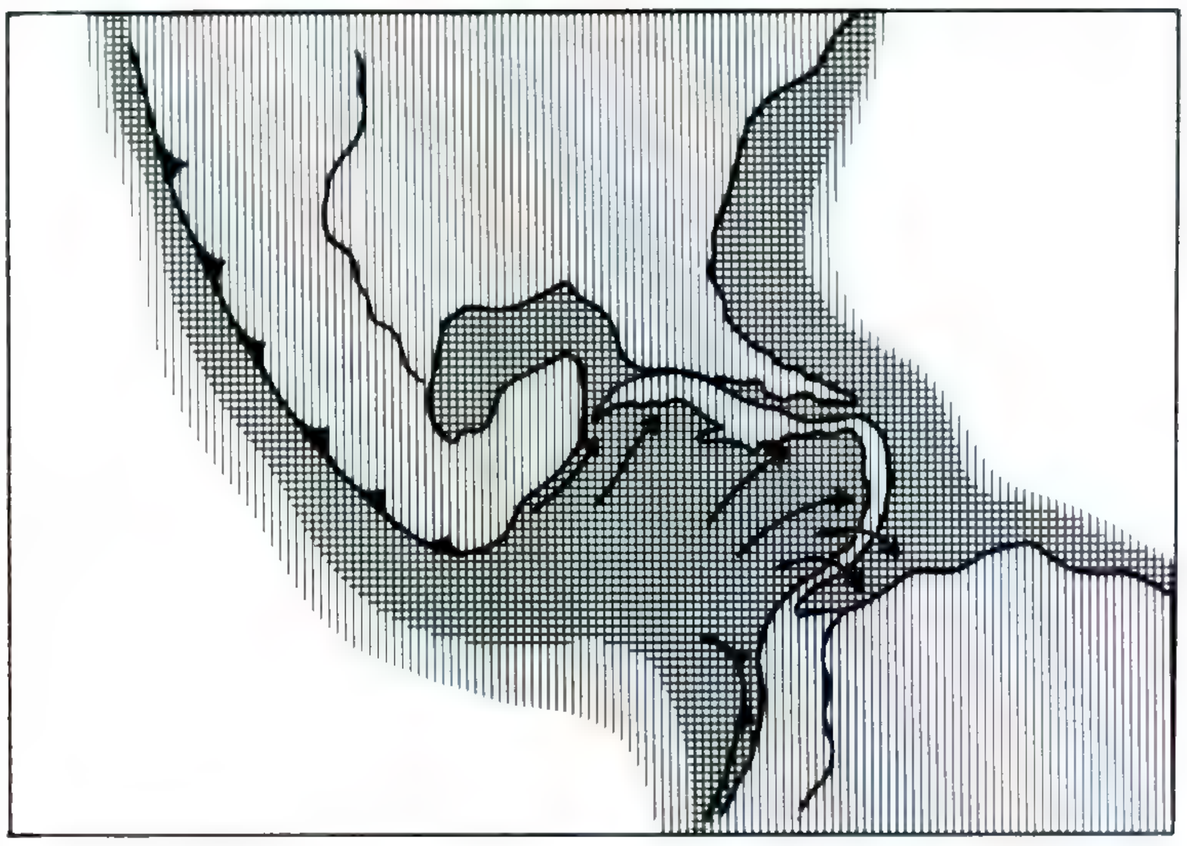


FIGURE 34. Eocene plate configuration (ca. 40 Ma) according to Dickinson and Coney (1980). A proto-Greater Antilles magmatic arc flips polarity of subduction to north facing as it transforms northeastward along the Yucatan escarpment and colliding with the Florida-Bahama bank where arc activity is extinguished.

cladistic constraint so that explicit branching diagrams represent present areas of endemism that can be shown to be congruent with a branching diagram representing a specific part of Caribbean geohistory. The branching sequence must also agree with the time constraints (relative times) of accretion and fragmentation.

CLADISTIC ANALYSIS

From the standpoint of Antillean history, the simplest place to begin is at that point 65 Ma when a proto-Antillean archipelago connected northern Central America (Yucatan) with northwestern South America (Figs. 33–44). This history can be divided into five components that will take us up to the modern period. In the earliest configuration (Fig. 33), the archipelago consists of 1) western Cuba and its sheared off fragments (Jamaica and southwestern Hispaniola) that are closely associated with northern Central America (Yucatan), and 2) eastern Cuba and its closely associated central Hispaniola. At this stage the Chortis block (Honduras-Nicaragua) is either Pacific land unconnected to northern Central America (Yucatan) or is sutured to western Mexico considerably to the north of the proto-Antillean archipelago.

Branching diagrams representing the complex history of the Caribbean must take into account both accretionary events, of which I identify seven since the main continental separation began about 165 Ma ago, and fragmentation events, of which I identify eight, including the initial continental separation.

Fragmentation events (roughly in order of decreasing age)

1. North America–Africa
2. North America–South America
3. Southern Mexico–North America

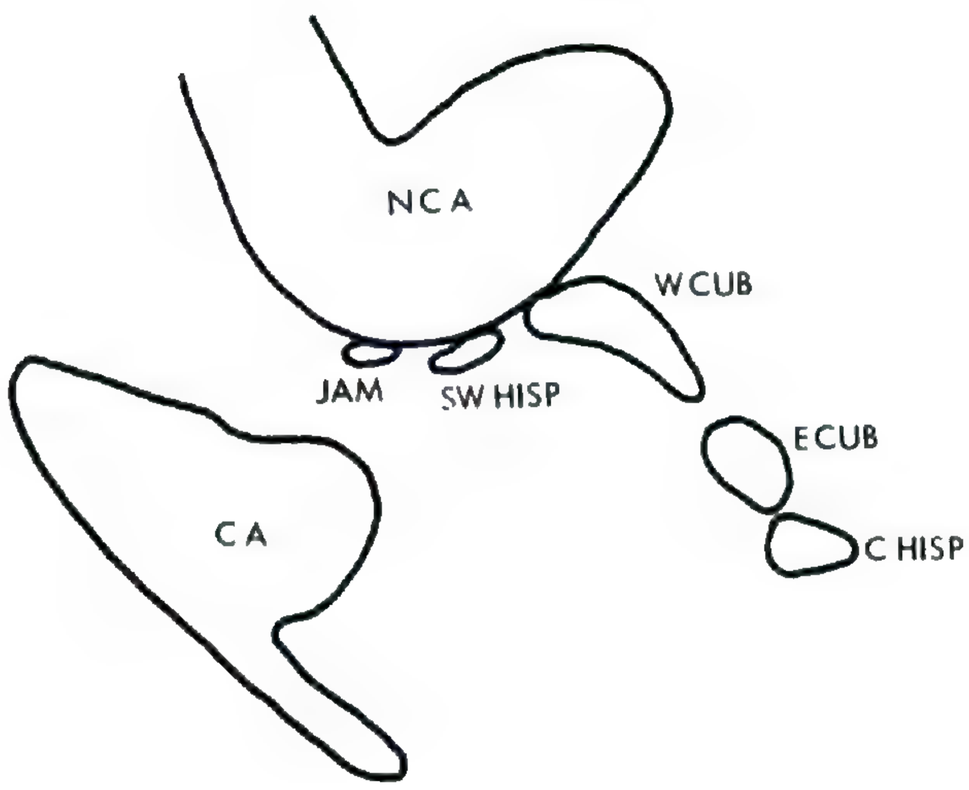


FIGURE 35. A diagrammatic consensus map of the mid-Cenozoic relations among some main components of the Caribbean heartland and a branching diagram that summarizes these relations.

4. South America–Africa
5. Southern Mexico (Yucatan)–western Cuba, Jamaica, southwestern Hispaniola
6. Eastern Cuba–Bahamas
7. Eastern Cuba–central Hispaniola
8. Hispaniolan Bahamas (fragment)–southern Bahamas

Accretionary events (roughly in order of decreasing age)

1. Yucatan–western Cuba, Jamaica, southwestern Hispaniola
2. Honduras, Nicaragua (?northern Costa Rica)–western to southwestern Mexico, and eventually to northern Central America (Yucatan)
3. Western Cuba–eastern Cuba
4. Eastern Cuba–central Hispaniola
5. Central Hispaniola–southwestern Hispaniola
6. Southern Bahamas (fragment)–central Hispaniola
7. Southeastern Costa Rica, Panama–northern Central America (Yucatan), northwestern South America

For the accretionary events there is an alternative model, differing in details of island sequence, and that is the one proposed by Carey (1958), recently discussed and illustrated by Nagel (1971, fig. 15) in which, in sequence from north to south, Jamaica, Puerto Rico, Hispaniola, and Cuba were a part of southern Mexico prior to their translation and rotation to a more easterly position. In this model the Bahamas lay between the tip of Florida and northern South America with an unspecified amount of intervening land, and Honduras-Nicaragua (the Chortis block), and the Yucatan (labelled Guatemala in Nagel's figure) were narrowly joined and both a part of the North American gulf coast. Also, in this model, it was the Lesser Antilles that formed an island arc connecting Mexico with South America in the early Mesozoic. From the standpoint of its relation to biogeography even this seemingly inverted model of land-area relationships yields the same general expectation of the biological relationships of the Caribbean subregions. The general features of the relation between Caribbean tectonics and biogeography were discussed most recently by Durham (1985), but primarily in connection with the model proposed by Sykes et al. (1982). If we adopt the position that land areas formed of mutually exotic terranes through accretion, might exhibit taxic area relationships when later fragmented, a consequential inference is that accretionary events might be followed by biotic transfer across the suture zone prior to secondary fragmentation and the differentiation of the now isolated ancestral population and its transferred descendants. If so, geological area cladograms used for comparison with biological area cladograms must incorporate both accreted and fragmented areas.

Since a suture zone might serve to isolate original and transferred biotic elements because of increasing geographic disruption during the later phases of suturing, my geologic area cladograms adopt the potentially most informative interpretation by incorporating sutured areas (that have not secondarily fragmented) on an equal basis with those that have secondarily separated.

Nevertheless, in a general cladogram of areas based on both fragmentation and accretion, land hybridizations would be represented either as reticulations (lines joining two or more branches)

or, as in the case of biological hybridizations, as unresolved branches representing the parent taxa and the hybrid. This is the conservative procedure adopted here. One might suppose that land hybridization (e.g., the Chortis block with southern Mexico, eastern with western Cuba, and eastern Cuba with central Hispaniola) would lead to a sharing of biotas by the joined fragments, but that supposition requires the subsidiary idea, probably correct in some instances but not others, that the suture zone presents no obstacle to biotic mixing. At least some suture zones seem perfectly hospitable to organisms, as in the case of the Chortis block suture zone (referred to as the Polochic-Motagua transform fault) where persistent, small-scale seismic activity, and the formation of a major down-dropped block of land (e.g., Lago Isabal) have not been inimical to the survival of faunal elements within the region [e.g., the poeciliid fishes discussed by Rosen (1979) and their occurrence on both sides of the Motagua-Polochic synclinal depression]. Other organisms, such as the swamp eels of the genera *Ophisternon* and *Synbranchus,* seem unusually sensitive to this fault line (see Rosen & Greenwood, 1975), although species of *Ophisternon* occur in the Yucatan and in Cuba, indicating that distributional boundaries cannot be assumed from geological data.

Even though one can identify at least 16 geographic areas involving Caribbean history (if the continental regions are included), I have chosen only eight of these to illustrate a method whereby geological data might be presented for comparison with biological data. The chief objective is to be able to relate a given biological distribution pattern to a specified period in Caribbean geohistory.

A geological area cladogram representing these relationships can be written as shown in Figures 35–43. The first cladogram (Fig. 35) is unresolved with respect to four areas [northern Central America (Yucatan), Jamaica, southwestern Hispaniola, western Cuba]. To make the most convincing case we will take the most conservative stance and derive from this general cladogram all possible completely resolved four-taxon statements, of which there are six shown in Figure 36. Many more three-taxon statements are derivable, but three-taxon statements have the disadvantage of representing relatively trivial statements of relationship and therefore requiring much more comparative data to demonstrate general congruence. For example, for three-area

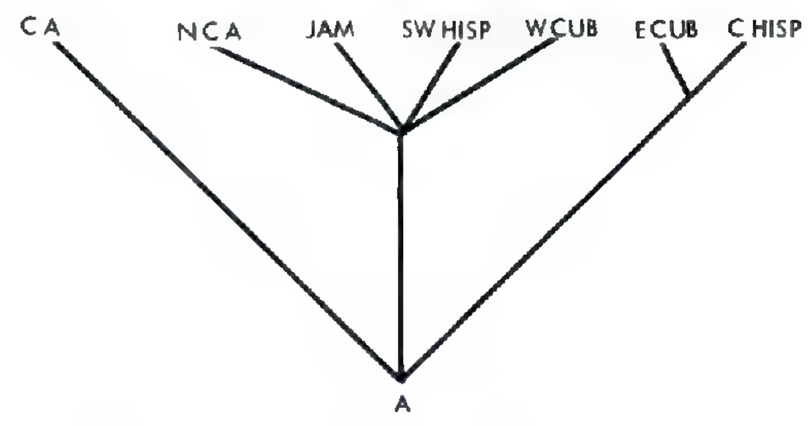
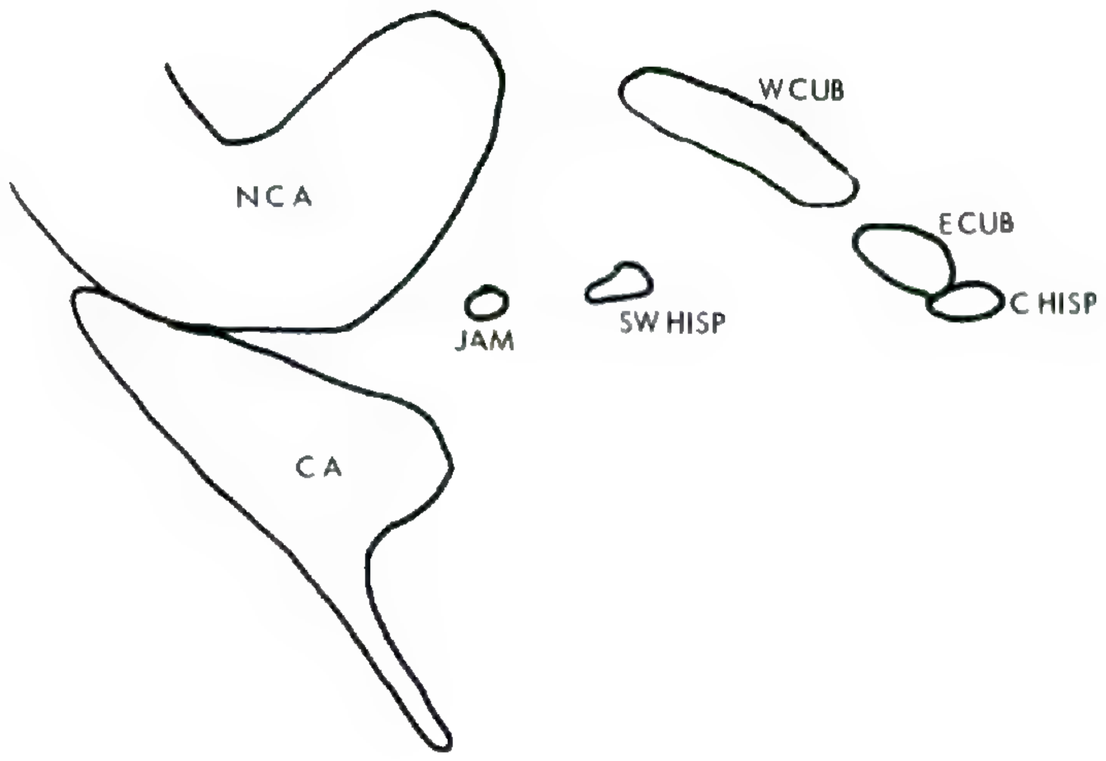


FIGURE 36. The branching diagram as in Figure 35 and the six completely resolved four-taxon, four-area statements derivable from it: CA, the Chortis block (southern Guatemala, Honduras, and Nicaragua); NCA, northern Central America (Yucatan); JAM, Jamaica; SWHISP, southwestern Hispaniola; WCUB, western Cuba; ECUB, eastern Cuba; CHISP, central or nuclear Hispaniola.

relationships there are only three possible solutions: A-B-C, A-C-B, B-A-C and two replications of one of these patterns would yield a probability that the congruence was ruled by chance once in every 27 trials (3 × 3 × 3), whereas there are 15 possible solutions to a four-taxon system (Nelson & Platnick, 1981; Rosen, 1978) and two replications of a given pattern would yield a probability of once in every 225 trials (15 × 15 × 15) that the congruence was random.

In the next geographic configuration in which the proto-Antillean archipelago begins to move eastward into the Caribbean region some of the earlier relationships are maintained (western Cuba, Jamaica, southwestern Hispaniola) and others are broken (western Cuba, Jamaica, southwestern Hispaniola) and a new association is established (the Chortis block with northern Central America). The general cladogram (Fig. 37) representing these relationships includes one land hybridization and three vicariant events and



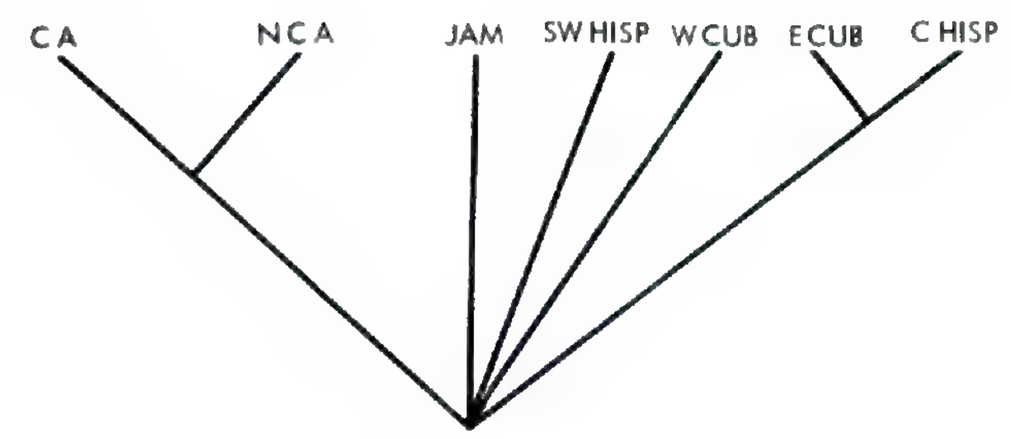
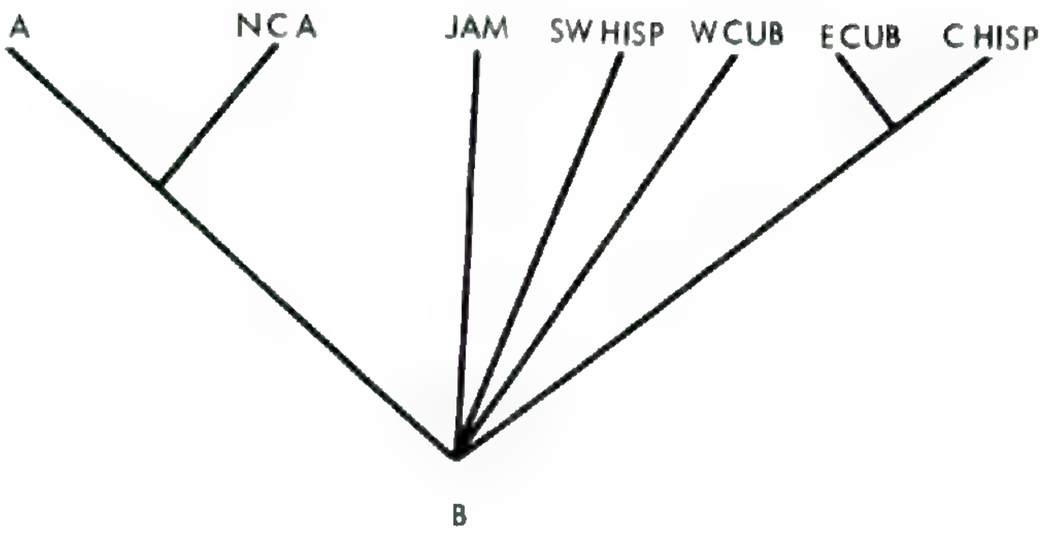


FIGURE 37. A diagrammatic consensus map of the late Eocene relations among some main components of the Caribbean heartland and the branching diagram that summarizes these relations.

includes a pentachotomy. From this general statement only a single resolved four-taxon statement is derivable (Fig. 38).

As eastward movement of the Antilles continues, central Hispaniola separates from eastern Cuba but western Cuba and eastern Cuba are joined (Fig. 39). This general cladogram also includes a tetrachotomy from which may be derived but a single resolved four-taxon statement (Fig. 40). Continued movement of the Caribbean plate brings southwestern Hispaniola and central Hispaniola into contact and, although no new mainland relationships are being established, the Chortis block continues to slide eastward against northern Central America (Yucatan) on the Motagua-Polochic fault so that at least new contiguous land-area-relationships are being established (Fig. 41). Here, too, the general cladogram includes a pentachotomy but gives rise to three resolved four-area cladograms (Fig. 42). In the modern configuration a new land contact is established between southern Bahamas and His-



Resolved four-taxon statements derivable from B :

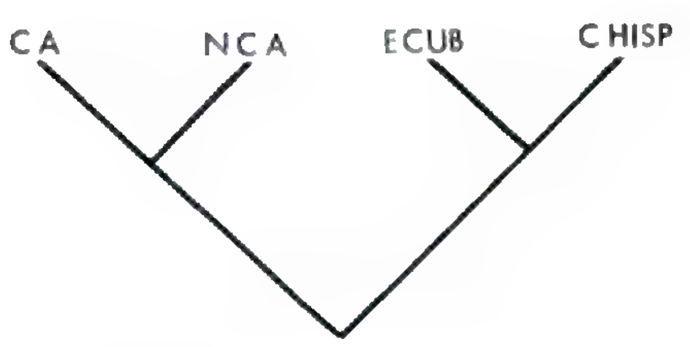
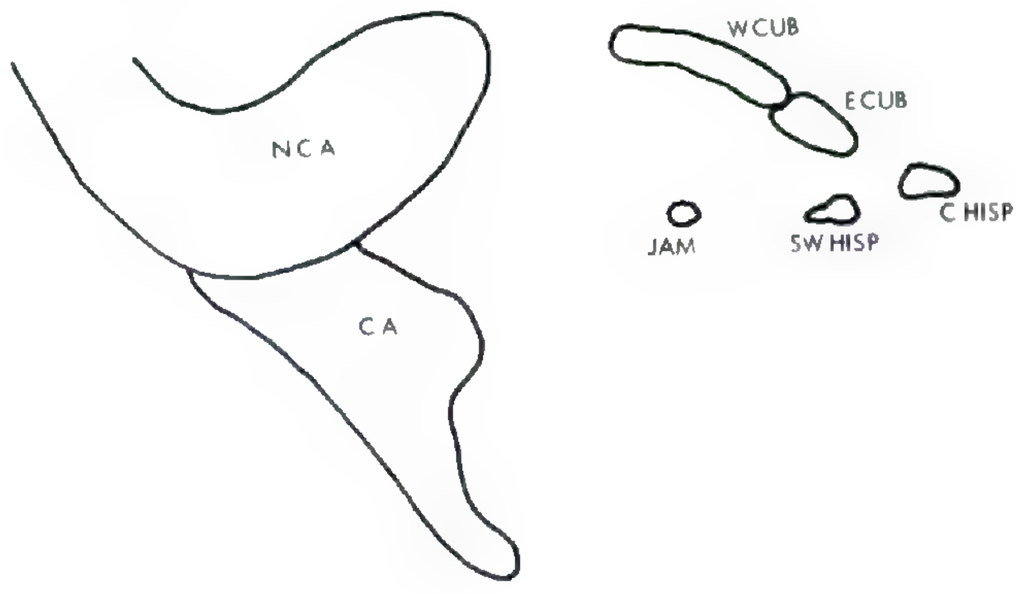


FIGURE 38. The branching diagram as in Figure 37 and the single, completely resolved four-taxon, four-area statement derived from it: abbreviations as in Figure 36.



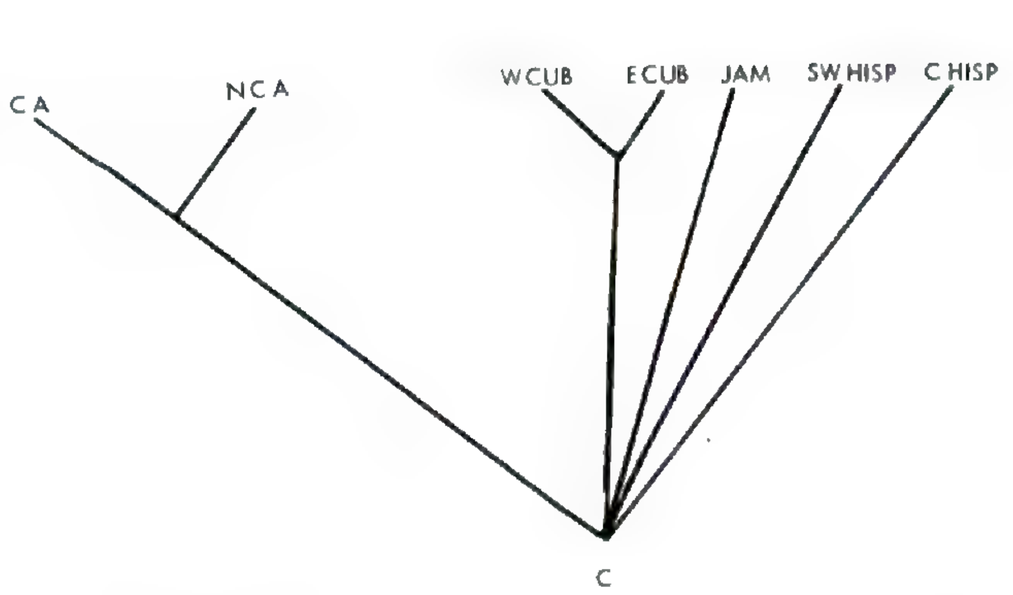
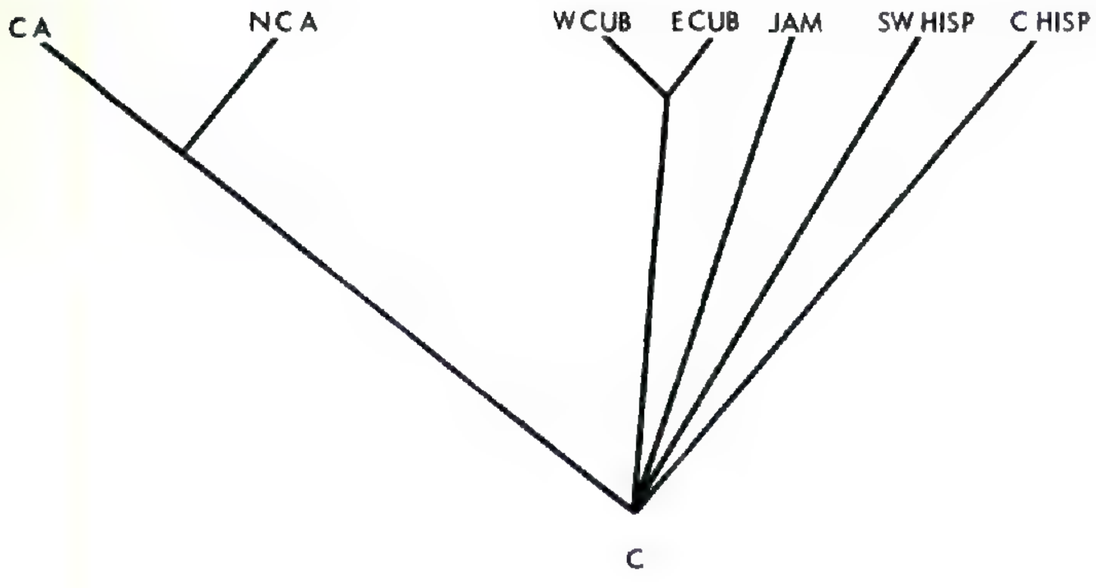
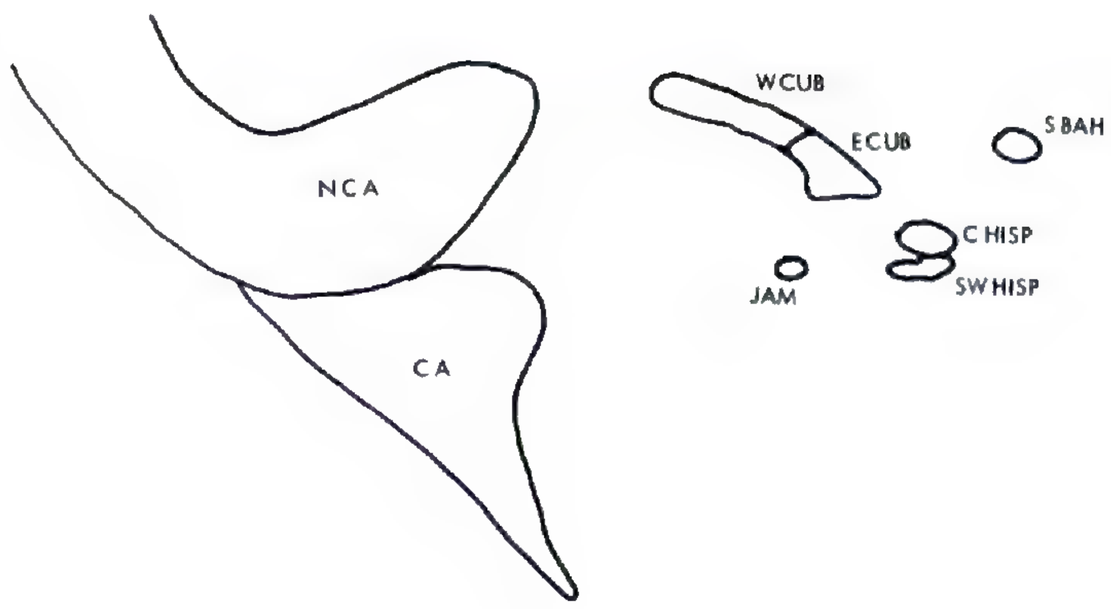


FIGURE 39. A diagrammatic consensus map of late Cenozoic relations among some main components of the Caribbean heartland and a branching diagram that summarizes these relations.





Resolved four-taxon statements derivable from C :

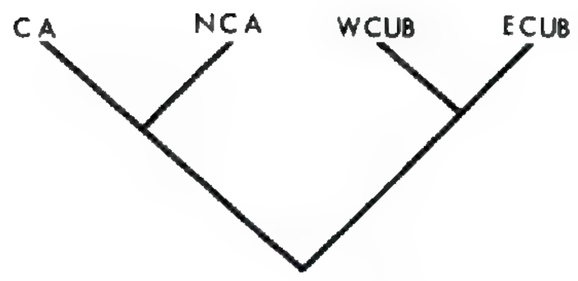


FIGURE 40. The branching diagram as in Figure 39 and the simple, completely resolved, four-taxon, four-area statement derived from it: abbreviations as in Figure 36.

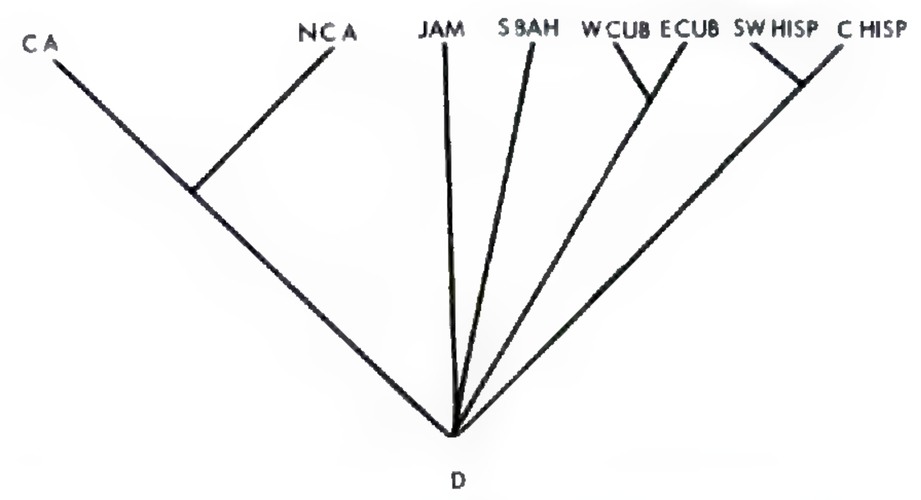
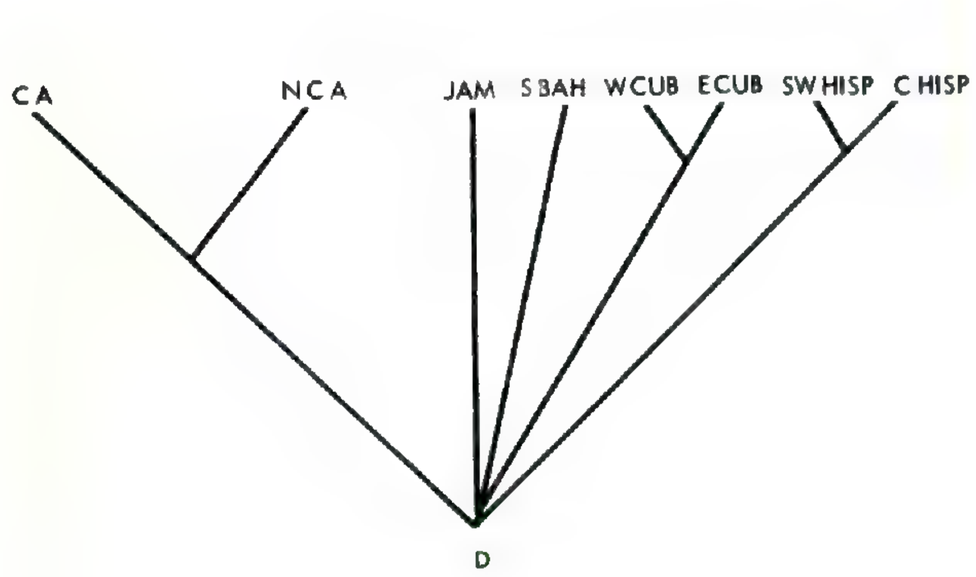


FIGURE 41. A diagrammatic consensus map of late Cenozoic relations among some main components of the Caribbean heartland and the branching diagram that summarizes these relations.

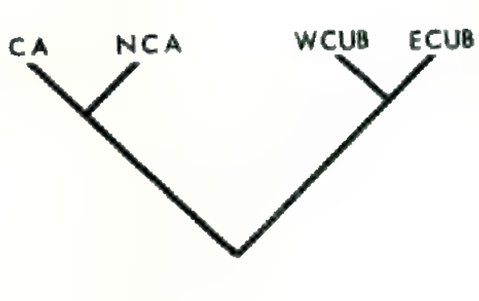
paniola, and the Chortis block continues to move eastward along the Motagua-Polochic fault. The general cladogram incorporates two dichotomies, one trichotomy, and one tetrachotomy (Fig. 43), but allows derivation of seven resolved four-area statements.

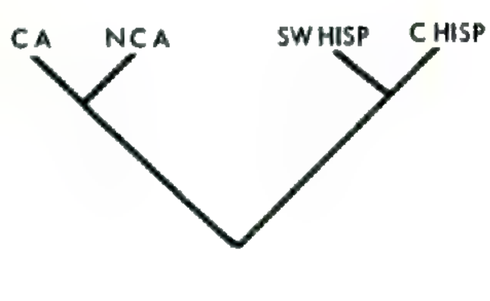
The sum of all of the proposed historical geologies leads to a number of predictions:

1. Hispaniola will have a mixture of elements, some related to the Bahamas, some to eastern Cuba, some to Jamaica, and others to northern Central America (Yucatan).
2. Some of the Antillean taxa will be parts of natural groups occurring in North and South America and Africa.
3. Honduras, Nicaragua, and perhaps western Costa Rica, will share related taxa in southern and southwestern Mexico, and some of these should be parts of more inclusive taxa that include the Antilles and South America.
4. The most inclusive taxa should have representatives in all the foregoing areas and in Africa.
5. Panama and eastern Costa Rica, by and large, should share species or species groups not unique to themselves but shared with South



Resolved four-taxon statements derivable from D :





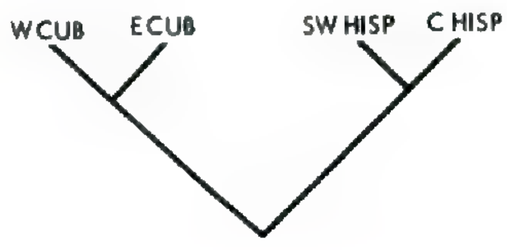


FIGURE 42. The branching diagram as in Figure 41 and the three completely resolved, four-taxon, four-area statements derived from it: abbreviations as in Figure 36.

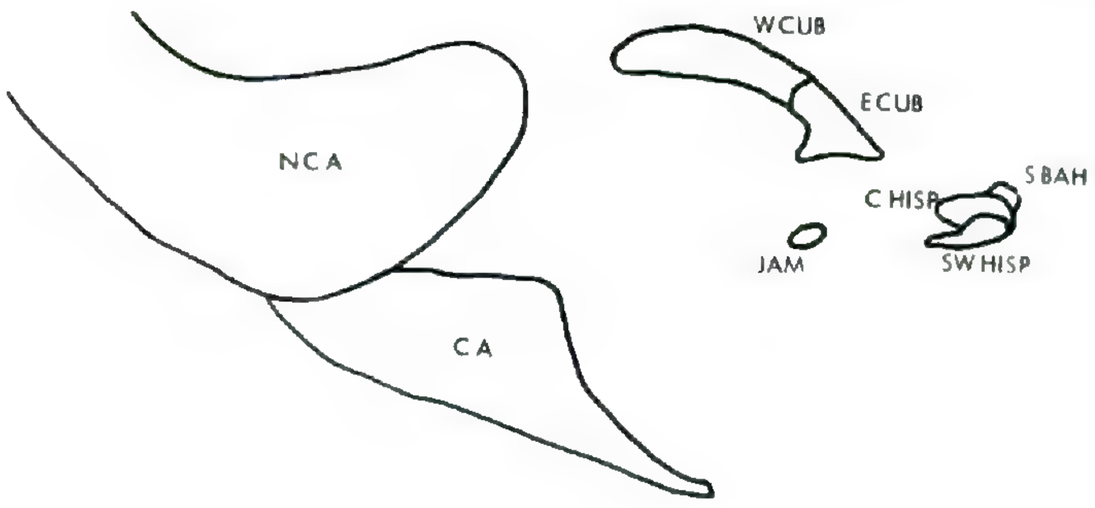


FIGURE 43. A diagrammatic map of the modern relations among some main components of the Caribbean heartland and a branching diagram summarizing these relations (SBAH, southern Bahamas).

America and southern Mexico and northern Central America (Yucatan).

6. Endemic sister taxa will be found in eastern and western Cuba on each side of the uplifted Cretaceous marine deposits at about 79° west longitude.

Whether the details of this geohistory are true or false is not at issue here. What is at stake is the possibility that a geohistory of this complexity might well have occurred, meaning that there might be 19 possible four-area cladograms with which biological area cladograms can be congruent. In other words 19 different cladistic solutions to organisms' interrelationships each might reflect the dramatic events in Caribbean geohistory.

In the recent past some authors (Rosen, 1976; Tolson, 1982) have assumed that failure to discover congruence between a biological area cladogram and a single simplistic interpretation of geohistory is license to consider that some dispersal may account for the lack of congruence. Tolson (1982), for example, assumed that the occurrence on Hispaniola of three boid snakes each with a different relationship to those on Jamaica, Puerto Rico, Cuba, and the Bahamas meant that dispersal might have occurred in order to permit the coexistence on one island of each of these endemics. But the complex history of Hispaniola should lead one to expect complex relationships of endemic Hispaniolan taxa.

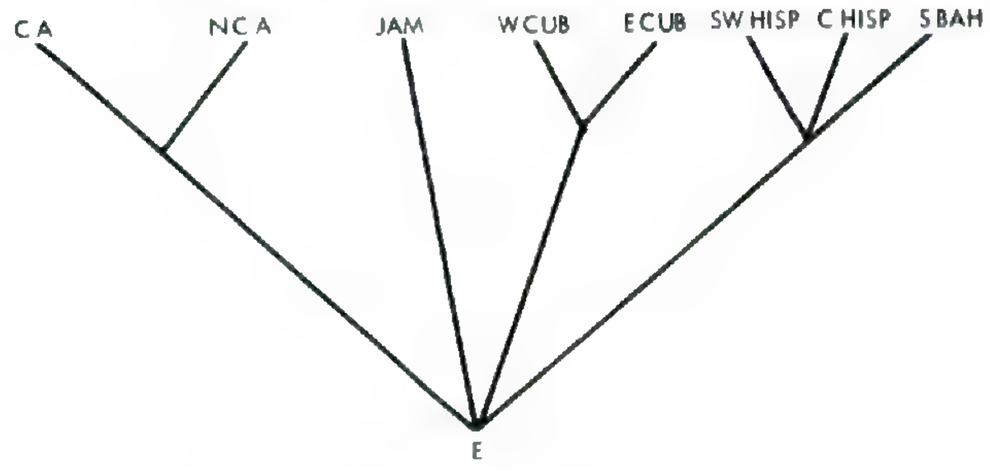


FIGURE 44. The branching diagram as in Figure 43 and the seven completely resolved four-taxon, four-area statements derived from it: abbreviations as in Figures 36 and 43.

The fact that several different historical geologies of the Caribbean specify similar kinds of complexities and support an origin of the Antilles from an ancient island arc between South America and northern Central America (Yucatan) is reason enough to suppose that land hybridization as well as fragmentation will yield a picture of unique endemism and mixed biotas in which endemic taxa from formerly isolated land fragments have been brought together in a way that conflicts with simple sister-group analysis.

There is a message here for all interested in biogeography and it is *not* that dispersal never occurs, but that theories of dispersal to explain biotic complexity are no more informative than theories of relationship based on symplesiomorphy, which widespread dispersed taxa resemble in biogeography (Nelson & Platnick, 1981).

Although geology has yet to fill in the details associated with the above five general cladograms, biology has a constructive role here because, by discovering congruent four-taxon area cladograms like the 19 derived above, it can independently support any one of the five general area cladograms and therefore details of geohistory that are still out of reach of geologists' data. If, in fact, there is a causal relation between an independent variable of geohistory and a dependent one of biohistory it should work just that way and biology should be at least as informative to the geologists as geology has been assumed to be for biologists in the past. Clearly biologists have always been ready to make that judgment since the last 150 years of biogeography has been based on the assumption that modern biotic distributions have been achieved through dispersal, signifying to geologists their belief that the relevant part of geohistory has been one of stabilism—a view that could have been challenged only by a theory of plate tectonics or a biological theory of general area congruence as proposed by Leon Croizat (1958, 1962).

In such detailed historical summaries of the geology of a region there is an unfortunate air of real knowledge, but Weyl (1980) has warned that, not only does the problem of reconstruction become increasingly difficult as we go back in time, but that the only criteria we have to go by are the data of prehistoric magmatism and the structure of the uppermost part of the crust, while the seismic and gravimetric data that are so important either are lacking or are poorly known relative to what is needed for establishing a detailed historical picture.

Even though one of the most detailed recent historical geologies (Sykes et al., 1982) is based on the paleoseismic data required by Weyl, biological data from the living and fossil biotas might have still more to say about Caribbean history. For example, if each of the 19 resolved four-taxon area cladograms were corroborated by a significant amount of taxonomic evidence, that general congruence would establish that the foregoing account was, indeed, the most probable geographic history of the region. But to accept as true the proposals of one geological model, and to abandon the search for cladistic area-congruence in favor of some a priori notion that all distributions might be explained by guesswork liberally laced with dispersalist intuition is to ensure that future generations of biogeographers will regard such proposals lightly. The fact that there are 19 resolved four-area cladograms that need to be corroborated might seem somewhat daunting to someone venturing for the first time into cladistic biogeography because it will, indeed, require a stupendous multidisciplinary effort to resolve decisive patterns for the region—and more still if one adds Mexico, North and South America, and Africa.

But I presume that if the problem were less difficult there would have been fewer attempts to describe nature by casual dispersalist scenarios about which almost no two scenario-writers can exactly agree, or provide that decisive constraint that shows one or another scenario to be flawed and scientifically unacceptable. But the history of today's biogeography has been characterized by the casual, almost offhand, manner of the scenario-writers that populate the field. Nevertheless, the temptation to propose imprecise, noncladistic, solutions to the problem of Caribbean history is great because of the abundance of endemic taxa that link certain areas. Patterson (1981: 458) complained that these seemingly reassuring biogeographic data add up to a phenetic concept that cannot lift biogeography out of its present narrative phase.

But all problems in comparative biology begin with a data gathering phase that incorporates unknown amounts of noise and signal. Cladistics identifies the signal. The need for cladistic vicariance analysis is underscored by questions such as those following.

How significant is the co-occurrence on Hispaniola of boid snakes in relation to a geological theory of a threefold origin for Hispaniola?

How significant is the occurrence of swamp eels of the genus *Ophisternon* restricted to Trinidad, Cuba, and northern Central America north of the Chortis block?

How significant are the occurrences of *Carlhubbsia* and *Quintana* plus *Girardinus* in northern Central America (Yucatan) and Cuba respectively (Rosen & Bailey, 1959) in relation to theories of ancient connections between western Cuba and the Yucatan?

How significant is the occurrence of related taxa of the poeciliid genus *Gambusia* in Cuba, the Bahamas, Hispaniola, and northern Central America (Yucatan) in relation to mid-Cenozoic interconnections of these areas?

These distributions, linking disjunct or hybrid areas, appeal to our sense of discovery. A cladistic analysis of areas will help us decide whether the distributional components that drew our

attention specify a general problem. I predict that such analysis, on a grand scale involving many different kinds of organisms, will corroborate some, if not all, of the five general geological area-cladograms that describe the longitudinal displacement theories of Caribbean history of Pindell and Dewey (1982), Sykes et al. (1982), and Wadge and Burke (1983). But, if such corroboration is not forthcoming, as biologists we are bound by the message of biological data in describing a biotic history of those geographic areas regardless of any possible conflicts with geologic theory.

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HISTORICAL ECOLOGY: A NEW APPROACH TO STUDYING THE EVOLUTION OF ECOLOGICAL ASSOCIATIONS

DANIEL R. BROOKS[1]

ABSTRACT

Historical ecology is presented as a complementary approach to evolutionary ecology. The prime distinction between the two approaches is the use of direct estimates of history in explanations by the former and of indirect estimates of history by the latter. Direct estimates of history are obtained by using phylogenetic systematics. They require analysis of many species simultaneously. Indirect estimates can be applied in individual cases and include such concepts as: (1) equating number of species in an ecological association with the age of the association; (2) equating the geographic range of a species with its age; and (3) equating the specificity of ecological interactions with the length of time species have been associated. Historical ecological methods have been applied in three general areas: (1) the historical context of geographic distribution patterns; (2) the historical context of ecological associations; and (3) the historical context of particular ecological life history traits. A unified quantitative approach allows historical ecological analysis for individual clades or aggregates of clades. Among the most interesting general conclusions that are forthcoming from the historical ecological perspective are those that differ from the evolutionary ecological view. These include: (1) ecological diversification lags behind morphological diversification historically; (2) degree of specificity is not a thoroughly reliable indicator of the age of an association; (3) resource tracking models of coevolution seem to include unacceptable assumptions; and (4) maximum competition scenarios are indistinguishable from random association scenarios. Future studies promise to be fruitful.

A number of fundamental and general questions have held the attention of ecologists for over a century. Why are species distributed in the manner they are? Why are certain species associated with each other ecologically, and how long have such associations existed? And, why do certain species have the ecological life history traits they do, and under what circumstances did those traits emerge? In the past 125 years, biology has operated under an evolutionary paradigm, a stance that I think has been undeniably productive. The search for causal mechanisms responsible for observed attributes has concentrated on evolutionary, that is historical, mechanisms. In ecology, this has led to the emergence of the field called evolutionary ecology.

In presenting what I will call historical ecology as a newly-emerging field, I do not wish to ignore the contributions of previous workers who were interested in problems of history and ecology. From the standpont of parasitology, at least, my views simply represent the most recent refinement of a tradition extending back over 90 years.

Von Ihering (1891, 1902) was impressed by faunal similarities between southern South America and Australasia and faunal differences between northern and southern South America. In the first study, von Ihering used data concerning the distributions of temnocephalid turbellarians and their crustacean hosts to postulate an ancient freshwater connection between South America and Australasia. He reasoned that if similar appearing hosts were inhabited by the same or closely-related parasites they were themselves closely related and not products of convergent evolution. In the latter study, von Ihering considered parasitic helminths in assessing the origins and evolution of South American mammals. He concluded the following: (1) North and South America were not connected in their present configuration until the Pliocene, (2) South American mammals include an autochthonous element, that originated and evolved in South America, and a heterochthonous element that invaded South America from the north subsequent to the Pliocene, (3) helminths of the autochthonous mammals are highly endemic whereas the helminths inhabiting the heterochthonous mammals include many occurring in other, Holarctic, mammals. Von Ihering asserted that data on host–parasite relationships in general constituted a ". . . valuable aid in analytical study of zoogeography and paleogeography."

Kellogg (1896) suggested that avian biting lice gave evidence of the genetic (= phylogenetic) relationships between their hosts. "The occurrence

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of a parasitic species common to European and American birds, which is not an infrequent matter, must have another explanation than any yet suggested. This explanation I believe is, for many of the instances, that the parasitic species has persisted unchanged from the common ancestor of the two or more now distinct but closely-allied bird-species" (Kellogg, 1896: 51). As examples, Kellogg (1913) listed shared mallophagan species in American and European avocets, coots and bitterns, American and Old World water-ousels and kinglets, and New World and Old World crows. Kellogg and Kuwana (1902) found that 19 of 44 (43%) mallophagan species collected from Galapagos birds also occurred on Central and North American birds.

An Australian student of avian mallophaga, Harrison (1911, 1914, 1915a, 1915b, 1916, 1922) considered host–parasite data significant for phylogeny reconstruction, using the same rationale as Kellogg. "Owing to both environment and food remaining unchanged through the centuries, these insects have not differentiated as fast as their hosts, and afford indications of original relationship between birds that have diverged widely from parent stock" (Harrison, 1911). Following the above-cited papers which concerned elucidations of avian phylogenetic relationships using parasite data, Harrison began using parasite data to support the notion of ancient Australia–Antarctic–South American land connections (Harrison, 1924, 1926, 1928a, 1928b, 1929). Harrison's work influenced some conclusions published by Johnston (1912, 1914, 1916) concerning phylogenetic relationships of hosts inhabited by the same or closely-related parasite species.

Metcalf, an American protozoologist, published a number of papers (e.g., 1920, 1922, 1923a, 1923b) in which he examined the paleogeographical and phylogenetic implications of opalinid ciliates and their anuran hosts. In 1929, Metcalf published a summary account of the ideas of von Ihering, Kellogg, Harrison, and himself, and concluded that all four had arrived at the same conclusions independently but that no one had added to the approach advocated by von Ihering. Therefore, he suggested that the appellation, "the von Ihering Method," was appropriate for studies of the historical relationships among hosts, parasites, and geography.

The above authors used a method based on occurrences of the same parasite in similar hosts in disjunct geographical regions. Fahrenholz (1913) discussed the phylogenetic significance of host–parasite relationships without regard for geographical distributions and without any assumption that hosts speciate while parasites do not. Fahrenholz (1913: 371) stated (author's translation): "From studies of parasitic mites in 1907, the question occurred to me: Is it possible to make definitive conclusions about their [hosts] phylogeny from the occurrence of the same or related parasites in different hosts? This statement should be answered in the affirmative. Because parasites are dependent, as living creatures, on their surrounding living conditions, so in general should the same type of parasite occur in the same type of host and with hosts of differing form the parasites should deviate from one another to the same degree as their hosts are related by kinship [verwandt sein]."

Hennig (1966) suggested that Fahrenholz considered host–parasite relationships a matter of general habitat preference and not phylogenetic phenomena. For example: "Obviously blood-sucking parasites—here the lice—must have particular dependence on the blood of the host so that the true lice (Anoplura) in varying hosts deviate from one another to a degree in the way the blood of the latter is different. Consequently, the lice would clearly mirror the blood relationships (Blutverwandschaft) of the respective host animals to a certain degree" (Fahrenholz, 1913: 372). Although the use of *verwanden* is ambiguous, I believe that Fahrenholz considered host–parasite information valid data relating to host phylogenies: "Thus one conclusion: on the grounds of the lice brought forward for discussion—in agreement with the blood studies—the catarrhine monkeys (Menschenaffen) stand much nearer to humans than to the remaining apes" (Fahrenholz, 1913: 374).

Thus, between 1891 and 1923 at least five workers arrived independently at similar conclusions, namely that host–parasite relationships were a manifestation of a phenomenon pertinent to phylogeny or historical changes. Subsequently, a number of authors attempted to explain parasite relationships in terms of hosts and formulated general "rules" about the evolution (= phylogenesis) of hosts and parasites (Andrews, 1927; Baer, 1948; Cameron, 1964; Darling, 1921; Dogiel, 1964; Dougherty, 1949; Eichler, 1941a, 1941b, 1948; Ewing, 1924, 1926; Hegner, 1928; Hopkins, 1942; Kirby, 1937; Manter, 1940, 1954, 1955, 1963, 1966; Metcalf, 1940; Pritchard, 1966; Stammer, 1957; Szidat,

1956, 1960; Zschokke, 1933). The rules form a small group of interrelated concepts:

1. Fahrenholz's Rule (see Eichler, 1941a, 1941b; Stammer, 1957; Cameron, 1964; Dogiel, 1964; Hennig, 1966; Ashlock, 1974): *Parasite phylogeny mirrors host phylogeny.*

2. Szidat's Rule (see Szidat, 1956, 1960): *The more primitive the host, the more primitive the parasites it harbors.*

3. Manter's Rules (see Manter, 1955, 1966; Inglis, 1971): (1) *Parasites evolve more slowly than their hosts;* (2) *the longer the association with a host-group, the more pronounced the specificity exhibited by the parasite group;* (3) *a host species harbors the largest number of parasite species in the area where it has resided longest, so if the same or two closely-related species of host exhibit a disjunct distribution and possess similar faunas, the areas in which the hosts occur must have been contiguous at a past time.*

4. Eichler's Rule (see Eichler, 1941a, 1941b, 1948; Inglis, 1971): *The more genera of parasites a host harbors, the larger the systematic group to which the host belongs.*

Two concepts of ecological associations appeared independently and nearly simultaneously, in systematics (von Ihering, 1891 and others discussed above) and in ecology (e.g., Verschaffelt, 1910; Brues, 1920). Almost immediately, specialists in each field found themselves in disagreement with each other regarding their understanding of the causes and manifestations of such associations (e.g., Dunn, 1925). This was due, in my opinion, to differences in interests or motivations coupled with a similar methodological approach. To a great extent, systematists were trying to record what had occurred between host group and parasite group during the course of phylogenesis. This was accomplished by describing as many associations as possible in terms of the hypothesis that members of the association exhibited congruent phylogenies. Often, the notion that such congruent phylogenesis was also related to changing geography was also included. Ecologists, however, were intent upon trying to determine if there was any historical (i.e., phylogenetic) significance to the interactions they observed. Most recent discussions have followed Ehrlich and Raven (1964), who asserted that such studies provide little data concerning phylogenies: "Although the data we have gathered permit us to make reasonable sequence predictions about phylogenetic patterns . . . , these predictions cannot be tested and the relationships cannot be specified further in the absence of a fossil record. The reconstruction of phylogenies on the basis of this sort of information would seem an unwarranted imposition on the data, since evolutionary rates and time are inseparable." Other ecologists had felt somewhat differently. Brues (1920: 315) wrote: "As we might *naturally* [emphasis mine] expect, it is possible to point out in a very general way a progressive specialization in the selection of food-plants which parallels to some degree what appears to have been the path of evolution among insects, as determined by the criteria furnished by comparative anatomy, development, and paleontology."

Between 1940 and 1966, the connection between systematics and ecology certainly became attenuated. The former assumed a progressively more passive role in evolutionary biology, summarizing the findings of the latter. There is a noticeable lack during this period, at least in parasitology, of direct comparisons between host and parasite phylogenies, and a steadily increasing reliance on degree of host specificity as the best indicator of historical association. In my opinion this was due to two different aspects of the emergence of neo-Darwinism as the prevailing evolutionary theory. The most obvious aspect is that neo-Darwinism is a theory of ecological determinism; various ecological factors operating on random variation produce historically contingent evolutionary change. Under such a paradigm the determination of close ecological interactions is much more important than matching phylogenies, whose congruence or lack thereof has little consequence for the theory. It is also possible that matching phylogenies seemed too much like directed evolution to many neo-Darwinists. Indeed, Kellogg wrote about the demise of Darwinism at the turn of the century and Metcalf was a leading spokesman for the American orthogenesis movement (Bowler, 1983). For whatever combination of reasons, attempts at explicit assessment of the historical components of ecological associations played a minor role during a period of more than 25 years.

Manter (1966) attempted to generalize host–parasite relationships further by describing parasites as a subset of the total characters of a given host species available for use in phylogenetic analysis. Hennig (1966) expressed similar views but considered symbiont data a form of "chorological" data to be fitted a posteriori to the host-group cladogram. He further stressed com-

parisons of parasite data and geographic distribution data (chorological data sensu strictu). Manter (1966) stated: "Parasites . . . furnish information about present-day habits and ecology of their . . . hosts. These same parasites also hold promise of telling us something about host and geographical connections of long ago. They are simultaneously the product of an immediate environment and of a long ancestry reflecting associations of millions of years. The messages they carry are thus always bilingual and usually garbled."

In 1972, H. H. Ross published two papers (1972a, 1972b) that dealt with explicit assessment of the historical context of ecological diversity in communities, especially of insects. Ross asked: "What are the ecological shifts which have occurred during phylogenesis?" "How do they arise?" and "How often do they arise?" By ecological shifts, Ross meant geographic and host changes, as well as changes in ecological life history traits. I consider these studies to comprise the seminal papers in the field which I will call *historical ecology*.

It will be my thesis in this review that evolutionary ecology as a field attempts to answer historical questions by using indirect estimates of history. This is not meant to be a criticism of evolutionary ecology. Rather, it is meant to provide a distinction that hopefully will make it possible to show that there is a place for a complementary approach. I will refer to this complementary approach as historical ecology, distinguished by virtue of its dependence on direct estimates of history in formulating evolutionary explanations for ecological associations.

I will begin by stating what I consider to be indirect and direct estimates of history. By indirect estimates, I mean such as the following: (1) equating the number of species in an ecosystem with the age of the system; (2) equating the geographic range of a species with its age; and (3) equating the specificity of ecological interactions with the age of the association denoted by the set of interacting species (see e.g., Boucot, 1983a). Direct estimates of historical aspects of ecology are achieved by the use of phylogenetic systematic methods. In the most recent past, a number of workers have suggested that use of phylogenetic systematic techniques could help investigations in historical ecology (Hennig, 1966; Michener, 1967; Ross, 1972a, 1972b; Ashlock, 1974). Thus, the distinction between the two approaches is not between qualitative and quantitative measures, because both approaches have quantified protocols. The rest of this review will explicate three general types of questions that can be addressed by historical ecology and will consider the extent to which such efforts do in fact constitute an approach complementing evolutionary ecology. The examples that I will present are drawn from my research on the helminth parasite faunas of lower vertebrates, but I hope to show that the principles involved can be extended to any type of ecological association.

I. How did species occurring in a given area come to be in that area?

This question encompasses two topics, the means by which a particular distribution was achieved and how long ago it took place. An historical answer can be provided for individual species or for entire community assemblages. I will provide examples of each.

One of the fundamental advances of the past 20 years in evolutionary biology has been the formal articulation of two different perspectives on the general manner by which species achieve their geographical distributions. These perspectives may be categorized loosely as the "island biogeography" paradigm (MacArthur & Wilson, 1967) and the "vicariance biogeography" paradigm (Croizat et al., 1974; Platnick & Nelson, 1978; Rosen, 1975, 1985). The first paradigm calls attention to the propensity for organisms to move about and the second reminds us that those movements may not be unconstrained. Among those most responsible for documenting the extent to which geographic distributions are not random assemblages were Cain (1944), Camp (1947), and Wulff (1950). In general, the perspective offered by both views is this: a species may be represented in a particular area because it evolved elsewhere and dispersed into that area, or it may occur in the area because it evolved there. In the first instance, the dispersal may have occurred a long time ago or relatively recently; in either case, there is no reason to expect the species' history to be coordinate with the history of the area into which it dispersed. In the second instance, the species' history must be coordinate with the history of the area.

It is at this point that an empirical distinction between evolutionary ecology and historical ecology can be seen. Evolutionary ecology may be limited to indirect measures of history but

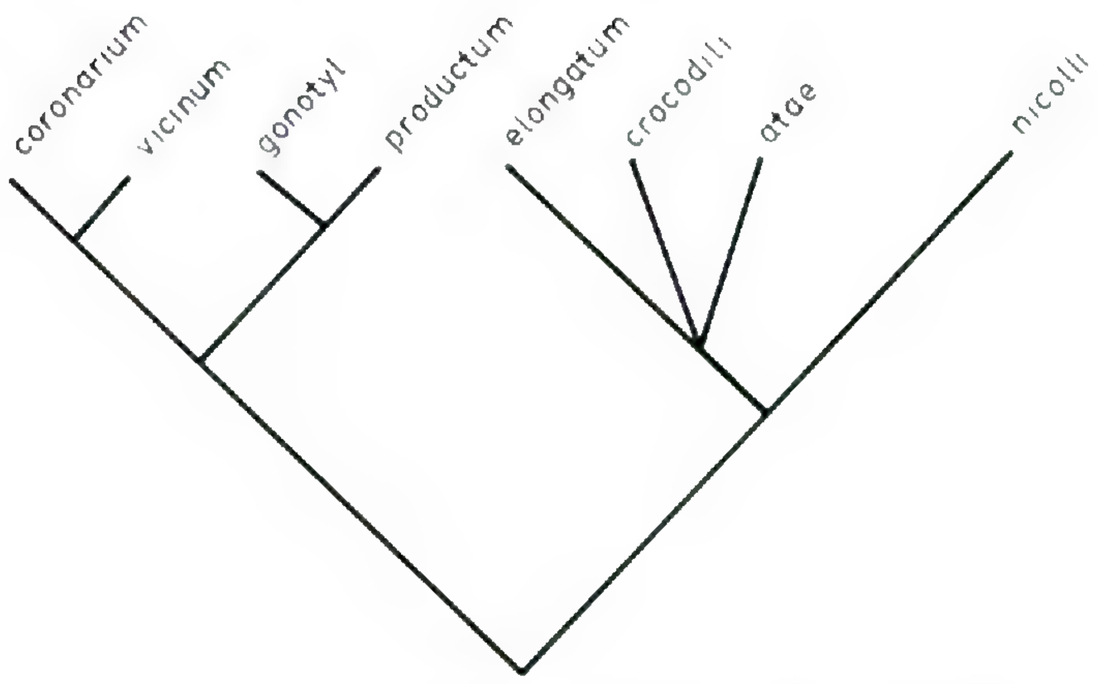


FIGURE 1. Cladogram depicting phylogenetic relationships of *Proctocaecum* species (redrawn from Brooks, 1981a).

these can be applied to a single species or a single ecological association. Historical ecology by contrast, can provide direct estimates of history, but only if a number of close relatives for each species represented in any given association are considered. Let us consider the following example.

The genus *Proctocaecum* comprises a monophyletic group of digenetic trematodes inhabiting the intestines of crocodilians. Figure 1 depicts a phylogenetic tree for *Proctocaecum* (see Brooks, 1981a). The relationships suggested by the phylogenetic tree can be superimposed on a map (Fig. 2) and the question of vicariance or dispersal can be asked. We note in Figure 2 that some of the contemporary species of *Proctocaecum* are separated from each other by ocean that crocodilians today do not traverse. In the case of these parasites, we also know that specific gastropod molluscs and some sort of small fish are required for completion of the life cycle; the dispersal abilities of any parasite are constrained by the least vagile of its hosts. If we look at past geographic configurations to find the most recent period in which dispersal of this group of parasites could be accomplished (Fig. 3), we notice that the sequence of speciation events suggested by the cladogram is coordinate with the geological history of the areas in which those species occur. This is highly suggestive that whatever dispersal might have occurred did not have an impact on the differentiation of species, which occurred in a manner coordinate with the history of the areas in which they now occur. In this example, our suspicion of vicariance, i.e., history, as the explanation for the geographic distribution of members of *Proctocaecum* is strengthened by observation that other digenetic trematodes inhabiting crocodilians exhibit the same distribution patterns (Fig. 4; see also Brooks, 1979a).

It is highly likely that many, if not most, ecological associations contain both vicariant and dispersalist elements. It is important to assess which components of an ecological association belong in each category in order to provide some assessment of the context in which particular interactions or ecological life history traits emerged. Historically associated lineages will all corre-

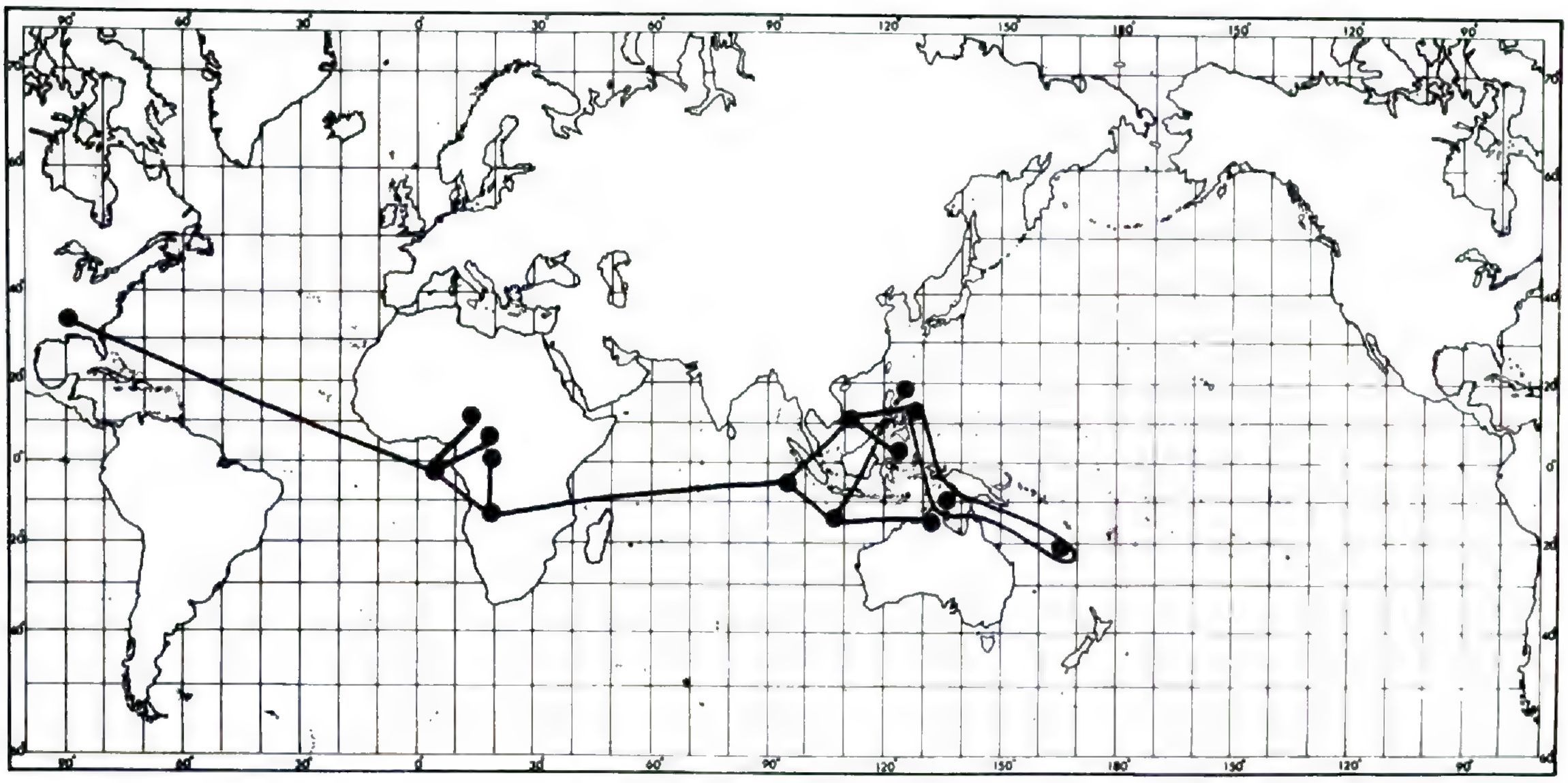


FIGURE 2. Cladogram depicting phylogenetic relationships of *Proctocaecum* species superimposed on map depicting contemporary geography (redrawn from Brooks, 1979a).

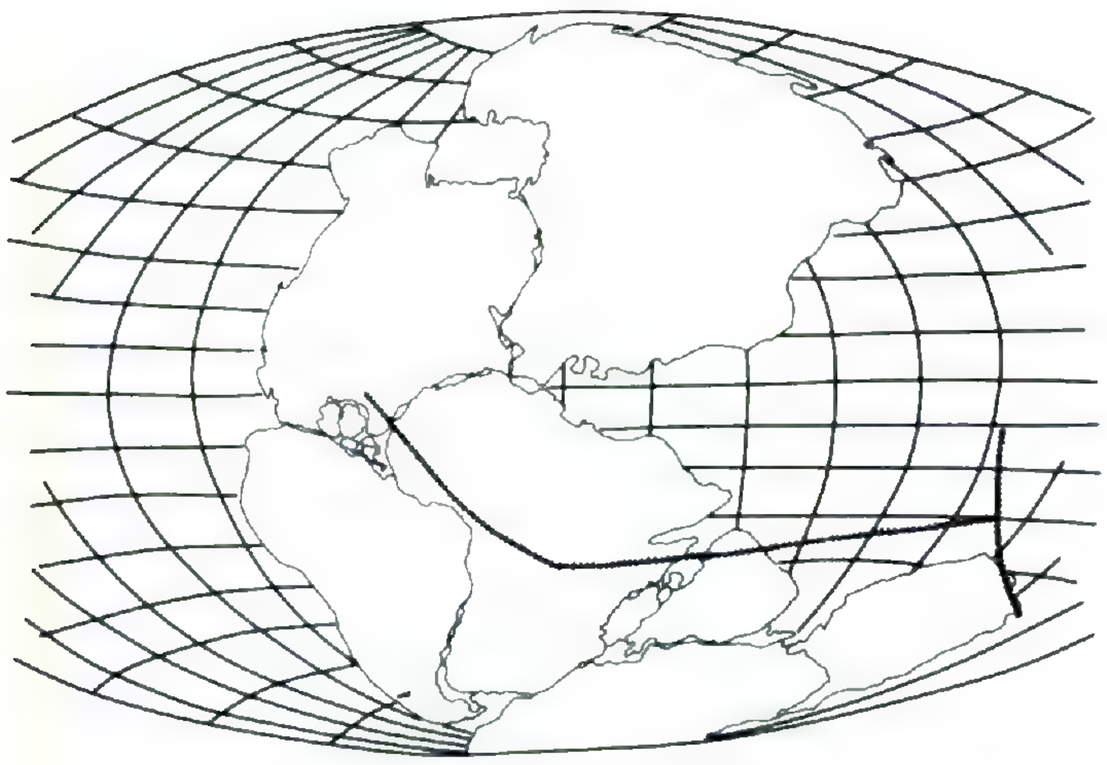


FIGURE 3. Distribution pattern indicated by phylogenetic relationships of *Proctocaecum* species overlaid on map depicting geography of the time period during which the study taxon could have achieved its present distribution (redrawn from Brooks, 1979a).

spond to the same set of interrelationships of the areas in which their component species now occur. Species that differentiated in other areas will support different patterns or relationships of areas. Any historically determined core of a given ecological association will be characterized by a set of species whose lineages have coordinate histories. Thus, it is not necessary to compare each lineage with geographic history, as one would if one were simply interested in historical biogeographic questions (cf. Rosen, 1985). Multi-lineage comparisons can be performed qualitatively (Platnick & Nelson, 1978; Nelson & Platnick, 1981; Rosen, 1985), or quantitatively.

The quantitative protocol has been presented by Brooks (1981b) and will be discussed in the next section as well. It is based on the notion

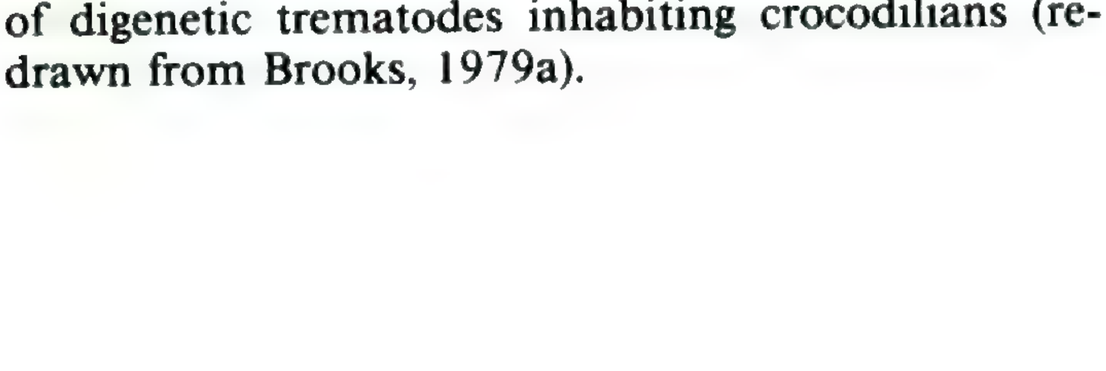
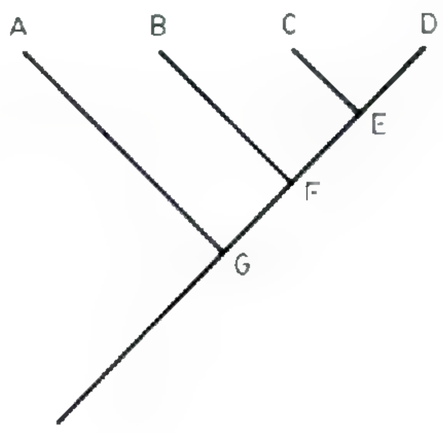


FIGURE 4. Generalized distribution patterns indicated by phylogenetic relationships of various groups of digenetic trematodes inhabiting crocodilians (redrawn from Brooks, 1979a).



a

	A	B	C	D	E	F	G
A	1	0	0	0	0	0	1
B	0	1	0	0	0	1	1
C	0	0	1	0	1	1	1
D	0	0	0	1	1	1	1
E	0	0	0	0	1	1	1
F	0	0	0	0	0	1	1
G	0	0	0	0	0	0	1

b

FIGURE 5. Conversion of a cladogram (a) into a matrix of binary variables (b).

that species can be considered characters of the areas in which they occur, and that lineages of species can be considered transformation series linking different areas in a historical pattern. Any given phylogenetic tree (Fig. 5a) can be converted into a matrix of binary characters (Fig. 5b) which can then be analyzed phylogenetically to indicate the pattern of relationships between the evolution of the clade and the areas in which the various known species occur. Any number of groups can be analyzed together using this technique, producing a summary statement of the historical context of the species composition in the ecological associations considered.

As an application of the above protocol, I have considered the parasitic helminths inhabiting neotropical freshwater stingrays and the areas in which they are known to occur [for a summary of the taxa, their phylogenetic relationships and their geographic distributions, see Brooks et al.

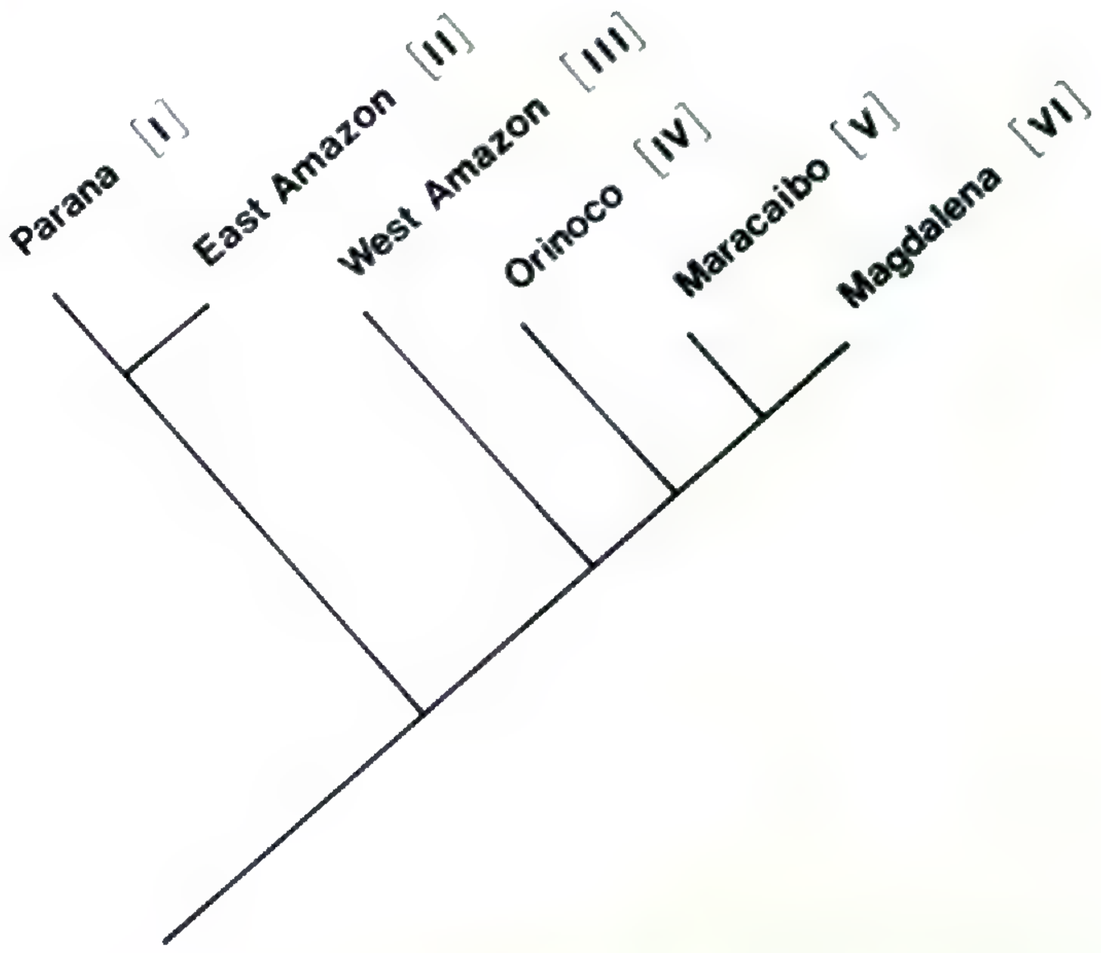


FIGURE 6. Summary cladogram depicting relationships among six areas (I–VI) in South America, based on phylogenetic relationships of helminth parasites inhabiting freshwater stingrays and living in those areas.

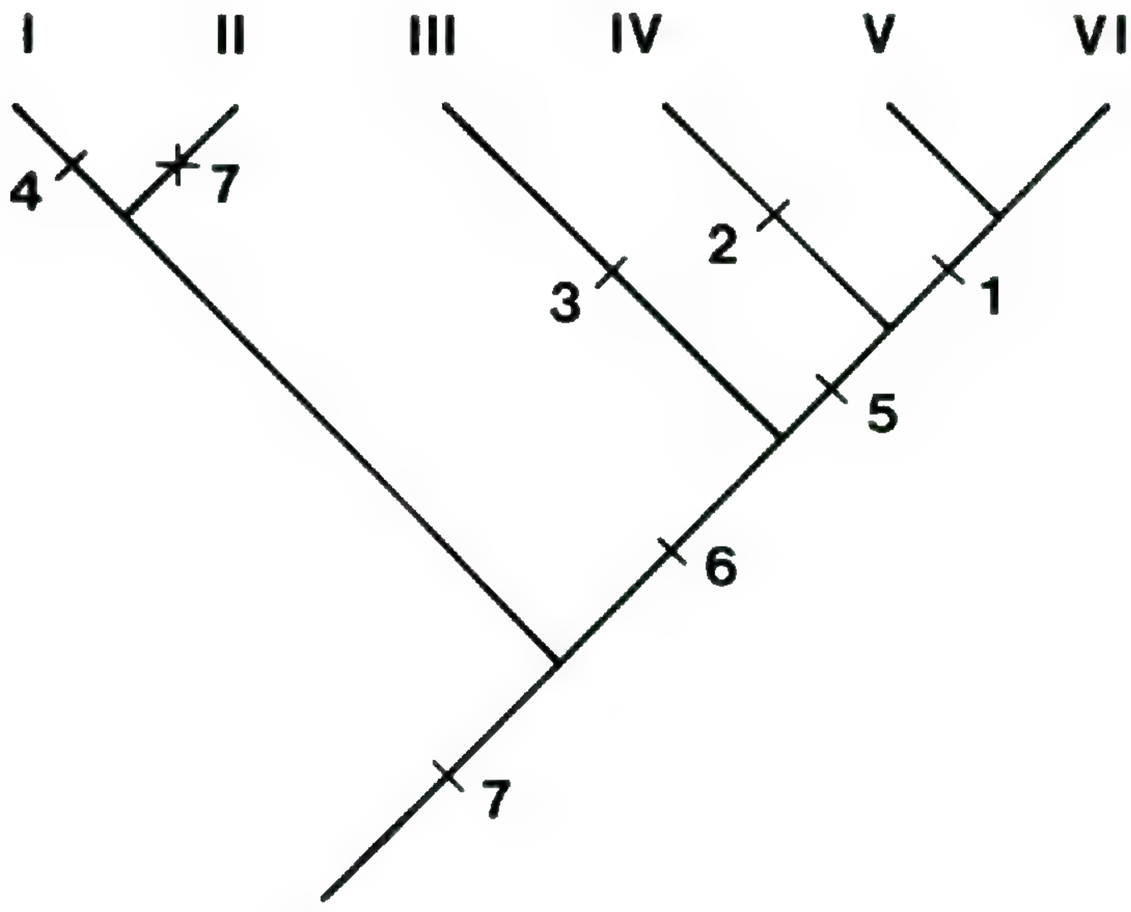


FIGURE 7. Summary cladogram from Figure 6 with numerical codes for genus *Acanthobothrium* indicated. 1 = *A. quinonesi*; 2 = *A. regoi*; 3 = *A. amazonensis*; 4 = *A. terezae*; 5 = common ancestor of 1 and 2; 6 = common ancestor of 3 and 5; 7 = common ancestor of 4 and 6. Slash marks accompanying numbers indicate presence in taxa; x mark indicates absence in area of predicted presence based on historical hypothesis.

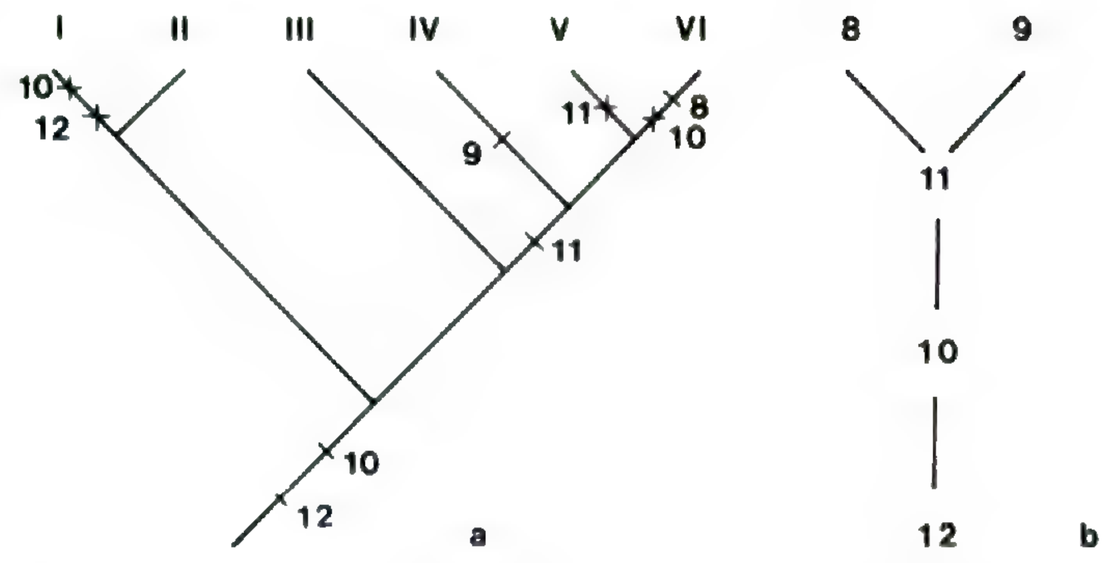


FIGURE 8. Summary cladogram from Figure 6 with numerical codes for genus *Potamotrygonocestus* indicated (a) and most parsimonious arrangement of numerical codes based on observed distributions (b). 8 = *P. magdalenensis*; 9 = *P. orinocoensis*; 10 = *P. amazonensis*; 11 = common ancestor of 8 and 9; 12 = common ancestor of 10 and 11.

(1981a), Brooks et al. (1981b) and Brooks (1981b)]. Figure 6 represents the relationships among six geographic areas based on the phylogenetic relationships of the parasites. Figure 7 shows the distribution of traits for a wholly vicariant group, the members of the genus *Acanthobothrium*. Each species (Nos. 1–4) and its inferred ancestor (Nos. 5–7) occurs only once on the cladogram, indicating perfect fit of the phylogenetic tree to the set of relationships among the areas. The only possible discrepancy (signified by 7X on area II) indicates a lack of any records for *Acanthobothrium* in area II (East Amazon). Based on the fit of the rest of the areas and *Acanthobothrium*, we would expect to find either *A. terezae* (4) or an undescribed species most closely related to *A. terezae* in area II. The distribution of members of *Potamotrygonocestus* (Fig. 8a), however, indicates a large amount of dispersal. Such dispersal can be inferred in two ways. First, there are four instances of observations (2 of 10X, one each of 11X and 12X) incongruent with the area relationships. Second, the phylogenetic tree for *Potamotrygonocestus* that best fits the observed distribution, shown in Figure 8b, suggests that taxon 10 is the ancestor of taxon 11. Phylogenetic analysis of the morphology of *Potamotrygonocestus* species places taxon 10 (*P. amazonensis*) as the sister-species of taxon 11, not its ancestor. Thus, this second view of the summary cladogram provides evidence of another historical incongruence between *Potamotrygonocestus* spp. and the areas in which they occur. This is due, apparently, mostly to widespread dispersal of *P. amazonensis*.

In the case of *Acanthobothrium*, of the 8 notations on the summary cladogram, 7 are congruent with its phylogeny, yielding a *consistency index* (Kluge & Farris, 1969) of 87.5%, whereas for *Potamotrygonocestus* the consistency index is only 4 out of 9 or 44.4%.

Below are summary statements about the evolution of the six communities.

Parana. There is no indication of colonization of Parana rays by parasites differentiated in other areas. Nor do we know of any local parasites that have expanded their habitats to include potamotrygonids. Of the six communities identified, this appears to be the earliest one differentiated (see Brooks et al., 1981b). Subsequently, there appears to have been a good deal of dispersal from the Parana to the East Amazon to the Orinoco following differentiation of the Parana fauna, but little dispersal into it.

West Amazon. This area also shows no indication of colonization of rays from other areas, or from local parasites normally associated with non-stingray hosts. It contains two species that are widespread in distribution. The Parana community is its closest, and apparently vicariant, relative.

Magdalena. With the exception of one species that also occurs in the Maracibo area, all known parasites found in stingrays in this area are endemics. This includes *Paravitellotrema over-*

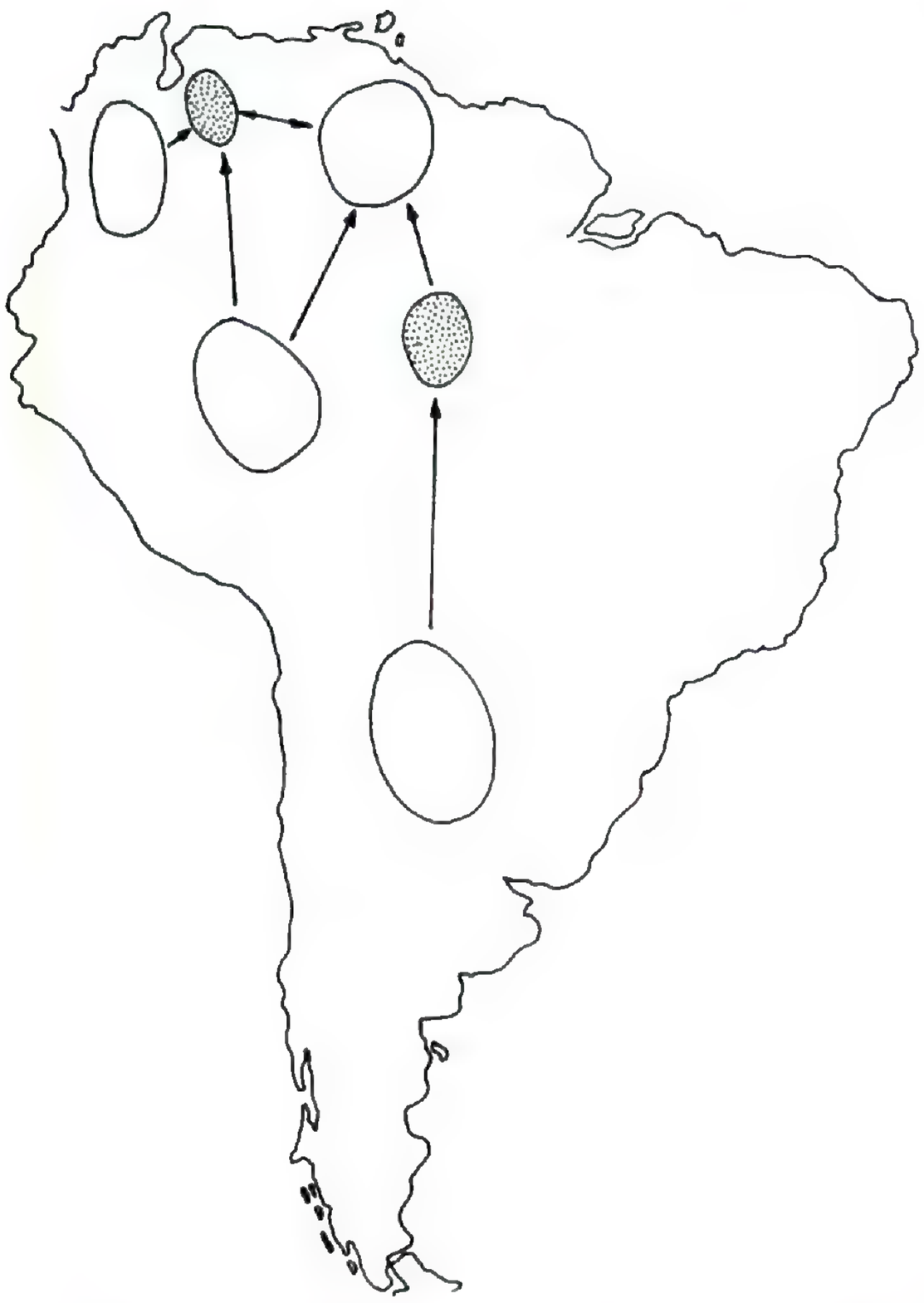


FIGURE 9. Summary of sources of community members for six communities of freshwater stingray parasites in South America. The four encircled areas represent communities having a substantial historical/coevolved core. The two areas indicated by shaded triangles are communities having at most a single endemic species. The arrows indicate non-historical contributions from one community to another. Refer to text for particulars.

streeti, which represents a group of digeneans normally parasitizing siluriform and characid teleosts. The other endemics apparently vicariated in the area, with one species dispersing into the Maracibo area.

The above three communities appear to be primarily vicariant communities some of whose members have dispersed into other areas. The next three communities present more interesting histories.

Maracaibo. This area has only a single, endemic, species of stingray. That stingray is known to host three species of helminth parasites, *Acanthobothrium quinonesi* from the Magdalena fauna, *Potamotrygonocestus amazonensis* from the West Amazon fauna, and *Rhinebothroides venezuelensis* from the Orinoco fauna. With apparent colonizing influences from three different communities, each with endemic species of *Acanthobothrium, Potamotrygonocestus,* and

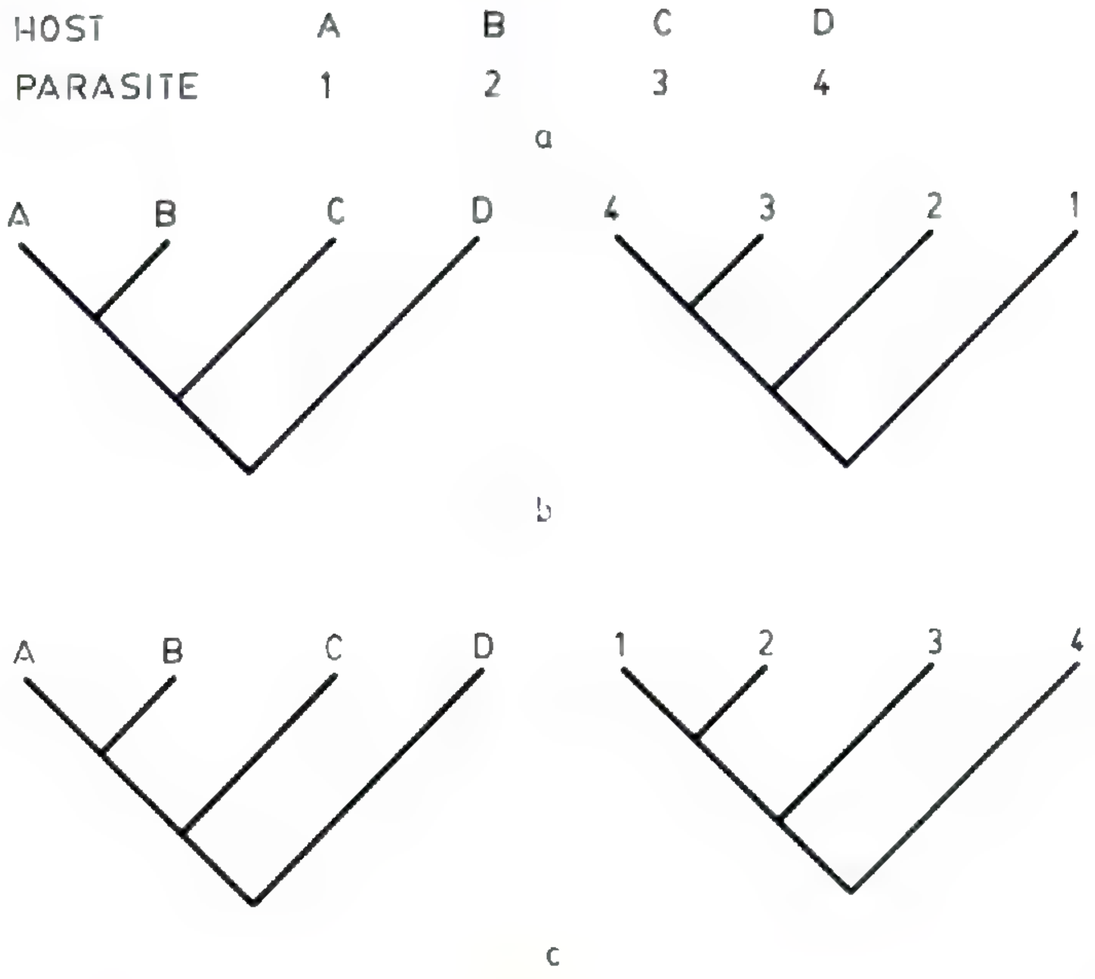
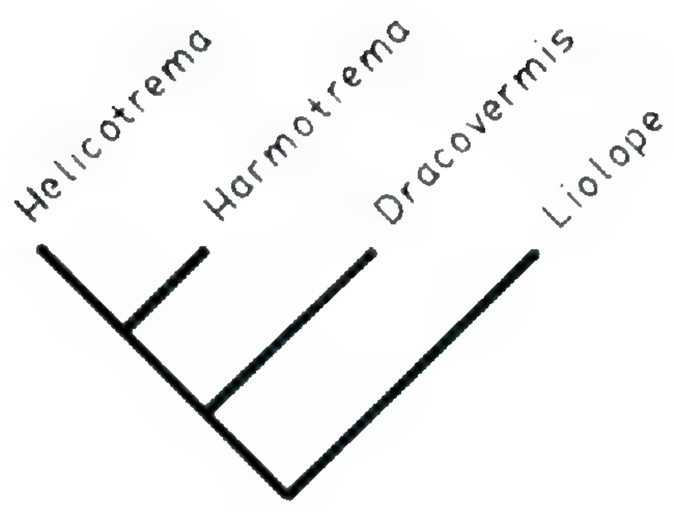


FIGURE 10. Observed associations between pairs of species (a), resulting from historical association (b), or from colonization (c) (redrawn from Brooks & Mitter, 1984).

Rhinebothroides, it is interesting that only a single species in each genus is established in the Maracaibo area. Perhaps this indicates something of the competitive abilities of the various parasites or perhaps it simply reflects uneven dispersal of suitable intermediate hosts. The latter seems more likely when Maracaibo is contrasted with the Orinoco (see below). The topology of the relationships among these parasites and their host does not differ from that in endemic areas.

East Amazon. There is only one endemic species of stingray helminth found in this area, *Rhinebothroides freitasi.* One other species is a colonizer from the West Amazon fauna. Several species have been acquired secondarily from local teleostean hosts. The rest are derived from the Parana fauna through dispersal. This community comes closest to being an "island biogeography" assemblage.

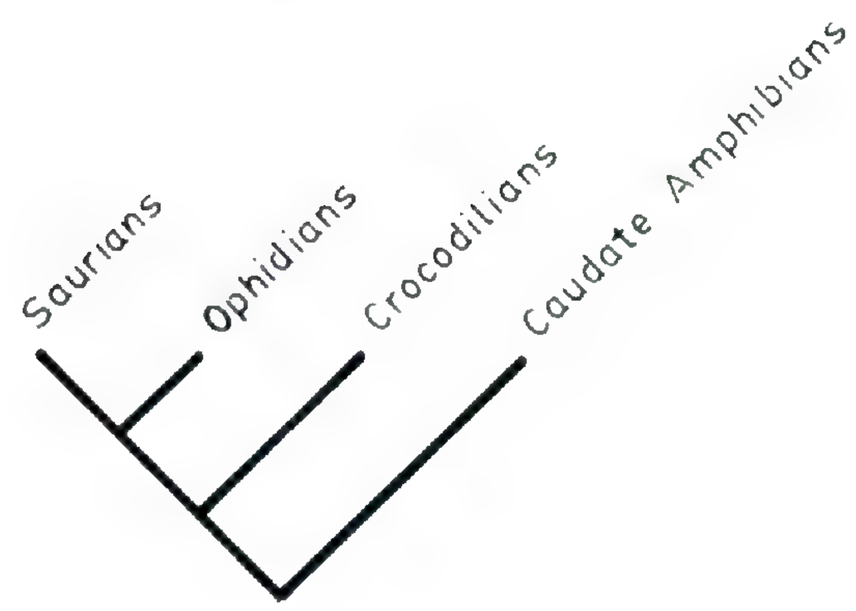
Orinoco. This area contains two different major faunas of potamotrygonid parasites, one derived through vicariance and one derived through dispersal from the Parana through the East Amazon with subsequent differentiation. To the first group belongs *Rhinebothroides venezuelensis, Potamotrygonocestus orinocoensis, Acanthobothrium regoi,* and *Echinocephalus daileyi.* To the second belongs *Rhinebothrium paratrygoni, Eutetrarhynchus araya,* and *Rhinebothroides scorzai* and *R. glandularis.* In contrast with Maracaibo, where a restricted fauna comprising a single species from three different faunas occurs, two faunas coexist in the Orinoco. If we



11 tested to by the fact that specimens of all three species of *Rhinebothroides* known from the Orinoco have been collected in a single host.

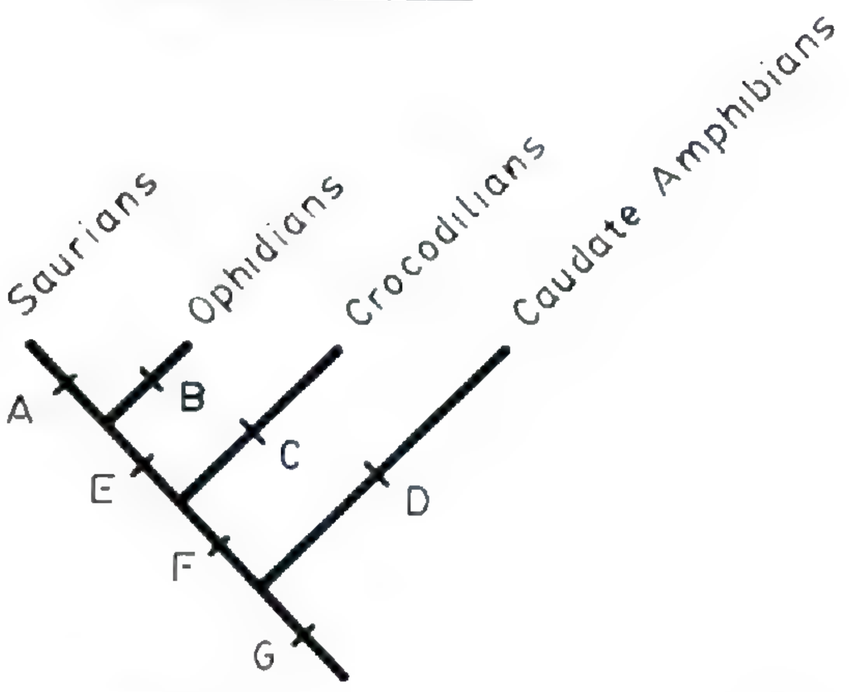
One difference between the Maracaibo and Orinoco faunas may be the occurrence of at least three species of potamotrygonid stingrays in the Orinoco and only one in Maracaibo. Brooks' (1981b) analysis of the host–parasite relation-

12 ships of potamotrygonids using the analytical technique described herein placed two of those hosts, *Potamotrygon hystrix* and *P. reticulatus,* in different parts of the cladogram (see Fig. 15). *Potamotrygon reticulatus* was related more closely to the Parana rays examined (*P. falkneri*), and *P. hystrix* was more closely related to *P. circularis* from the West Amazon. The Orinoco thus acts like two or three communities that have joined to form a larger community. Figure 9 summarizes the sources of components in these various communities.



	A	B	C	D	E	F	G
A	1	0	0	0	1	1	1
B	0	1	0	0	1	1	1
C	0	0	1	0	0	1	1
D	0	0	0	1	0	0	1
E	0	0	0	0	1	1	1
F	0	0	0	0	0	1	1
G	0	0	0	0	0	0	1

13 Evolutionary ecologists are interested in the effects of different kinds of ecological phenomena, such as colonization, competition, and sympatric speciation. Information of the sort provided by this kind of study could be used to identify effective ecological associations that owe their present configuration to different processes.



14 II. How do two or more species with a "close and evident ecological relationship" (sensu Ehrlich & Raven, 1964) come to be related that way?

This is the question addressed by the concept of coevolution as defined by Brooks (1979b), Mitter and Brooks (1983), and Brooks and Mitter (1984). Associated species (Fig. 10a) may be so because they inherited an ecological relationship from their ancestors; this is a state of *association by descent.* Alternatively, species may be associated presently but differentiated prior to their association; this is *association by colonization.* In the first case, the histories of the two associates will be coordinate (Fig. 10b) and, in the second, they will not be coordinate (e.g., Fig. 10c).

One type of ecological association for which such evidence is fairly abundant is that of host–parasite associations. For example, Figure 11 depicts the relative phylogenetic relationships of four groups of vertebrates, and Figure 12 is a cladogram of four genera of closely related digenetic trematodes. Following the method of Brooks (1981b), the parasite cladogram can be considered a character-state tree, or transfor-

FIGURES 11–14. Documenting degree of historical association between members of ecological associations.—11. Cladogram of four genera comprising the trematode family Liolopidae.—12. Cladogram representing phylogenetic relationships of hosts for liolopids.—13. Matrix of binary characters representing cladogram (a) in Figure 10.—14. Host relationships predicted by phylogenetic relationships of their liolopid parasites (redrawn from Brooks, 1981b).

include the occurrence of *Potamotrygonocestus amazonensis* from the West Amazon fauna via dispersal, and the occurrence of *Megapriapus ungriai* from local teleosts, more than two faunas coexist. That this coexistence is real may be at-

mation-series (Hennig, 1966), of the host group, converted into a matrix of binary codes (Fig. 13), and used to classify the hosts (Fig. 14). Points of agreement between host phylogeny and parasite-derived host relationships support association by descent; points of disagreement represent episodes of colonization. Note the parallels between the documentation of historical and non-historical associations between species and the documentation of historical and non-historical geographic distributions.

This parallel can be extended to include analysis of more complex systems than two-species interactions. Consider a multi-species ecological association. Those having historical associations will all have coordinate histories, whereas colonizers will each have a unique connection with the association. Figure 15 presents two different groups that have slightly different speciation patterns but that both have historical associations with the same host group. Note that the host relationships postulated by both parasite groups are the same. For any parasite fauna, or for any multi-species ecological association, the pattern of host relationships supported by coordinate parasite phylogenies will be coordinate with the host phylogeny. From a summary cladogram produced in this manenr (e.g., Fig. 16), summary statements about the historical components of an ecological association can be produced. The digenetic trematode fauna of crocodilians, for example, comprises many species acquired by colonization from predatory fish (through ingestion of common intermediate hosts). Despite this, analysis of the total fauna either qualitatively (Brooks, 1979a) or using the method discussed above (Brooks, 1981b) shows agreement with the host group phylogeny. Recently, a student in my laboratory (O'Grady, unpubl. data) has shown that the phylogenetic relationships of nematode parasites of crocodilians, which also include a number of colonizers, produce a summary statement of host relationships coordinate with host phylogeny.

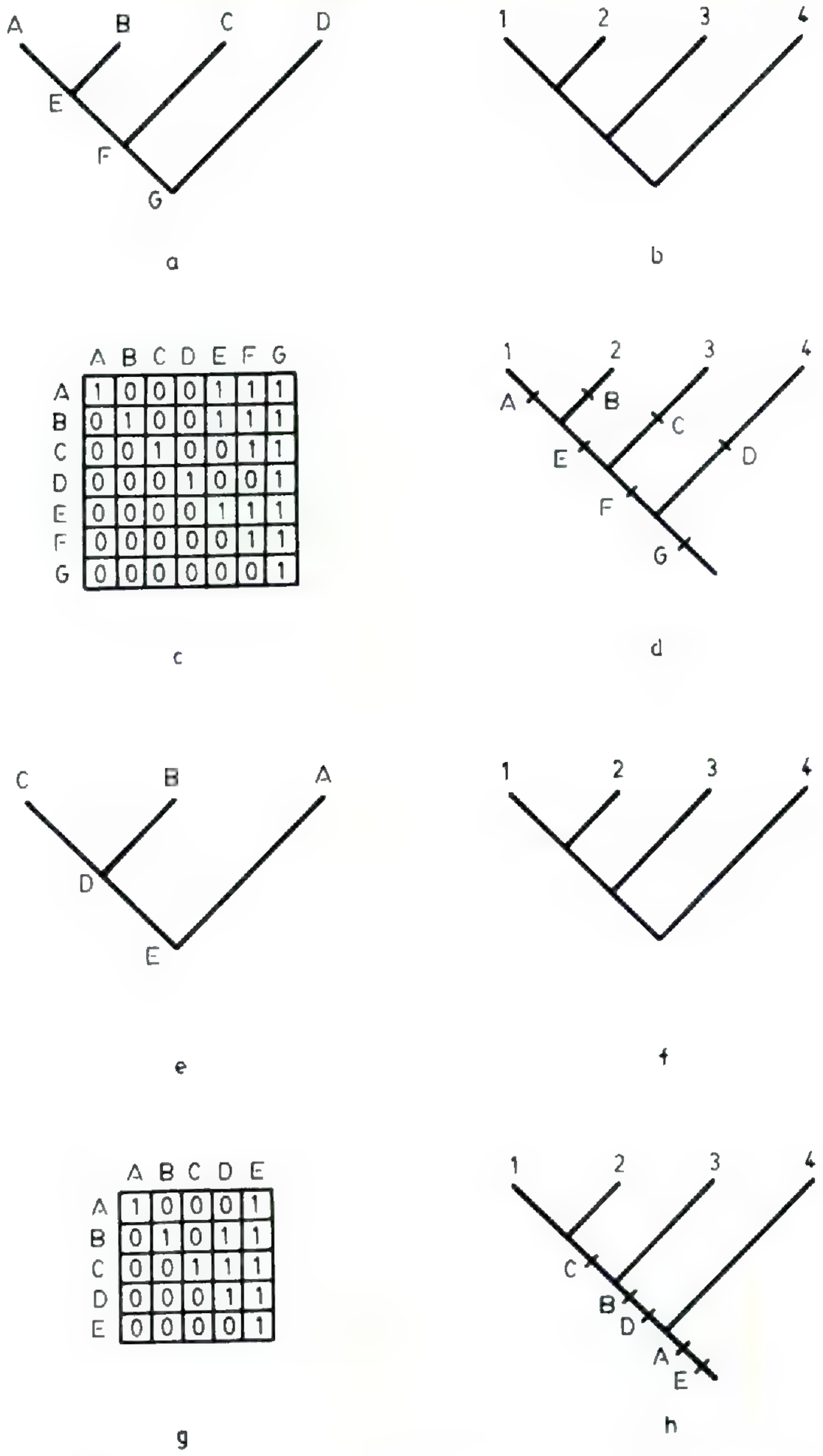


FIGURE 15. Finding congruent historical aspects of ecological associations. (a) and (e) are cladograms for groups of taxa associated with another group [(b) and (f)], (c) and (g) are binary matrices representing cladograms in (a) and (e), (d) is a cladogram depicting fit of phylogenetic relationships of the group in (a) to the group in (b), and (h) is a cladogram depicting fit of phylogenetic relationships of the group in (e) to the group in (f) (redrawn from Brooks, 1981b).

Before moving on to the third area of discussion, I would like to mention an alternative quantitative approach. This is the "nearest neighbor" method of Mickevich (1981), introduced as a tool in analytical biogeography. In his study of crocodilian nematodes, O'Grady (unpubl. data) compared results obtained using both Brooks' (1981b) and Mickevich's (1981) methods. The results were the same in both cases. Thus, it appears that there is a unified quantitative approach, at least implicitly, available for studies of historical ecology.

III. Under what conditions did the ecological life history traits that we observe today emerge?

This category provides historical ecological contributions to questions concerning the evolutionary effects of competition and the occurrence of adaptive radiations. It allows possible distinction between factors responsible for the maintenance of traits seen today and factors responsible for the emergence of those traits in the

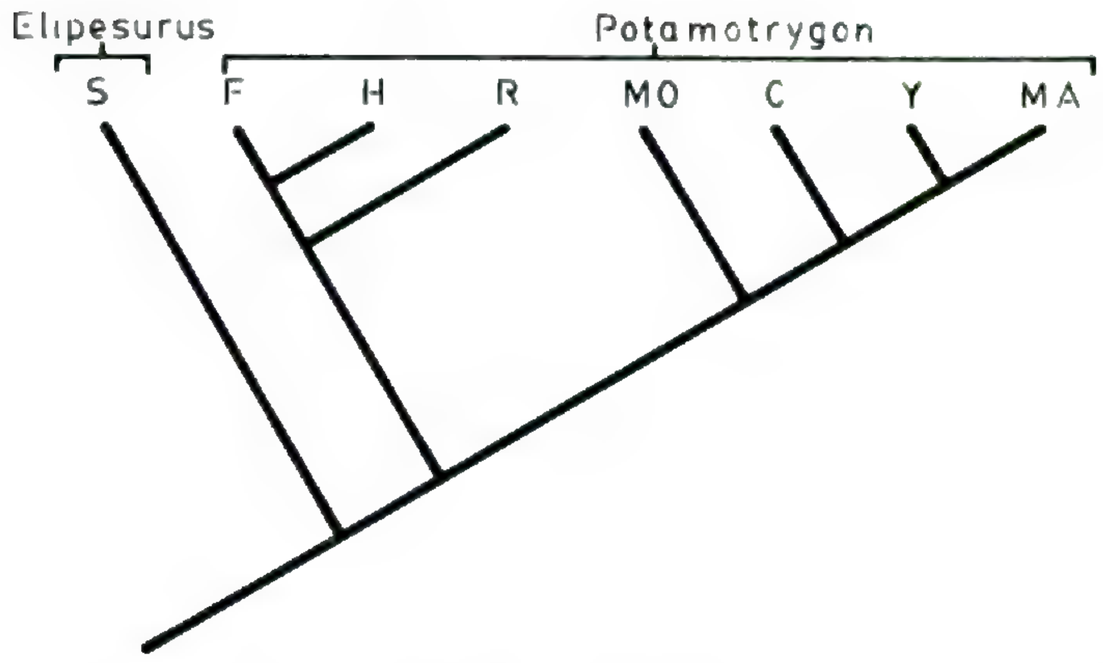


FIGURE 16. Cladogram depicting phylogenetic relationships among eight species of neotropical freshwater stingrays based on the phylogenetic relationships of their helminth parasites (redrawn from Brooks, 1981b).

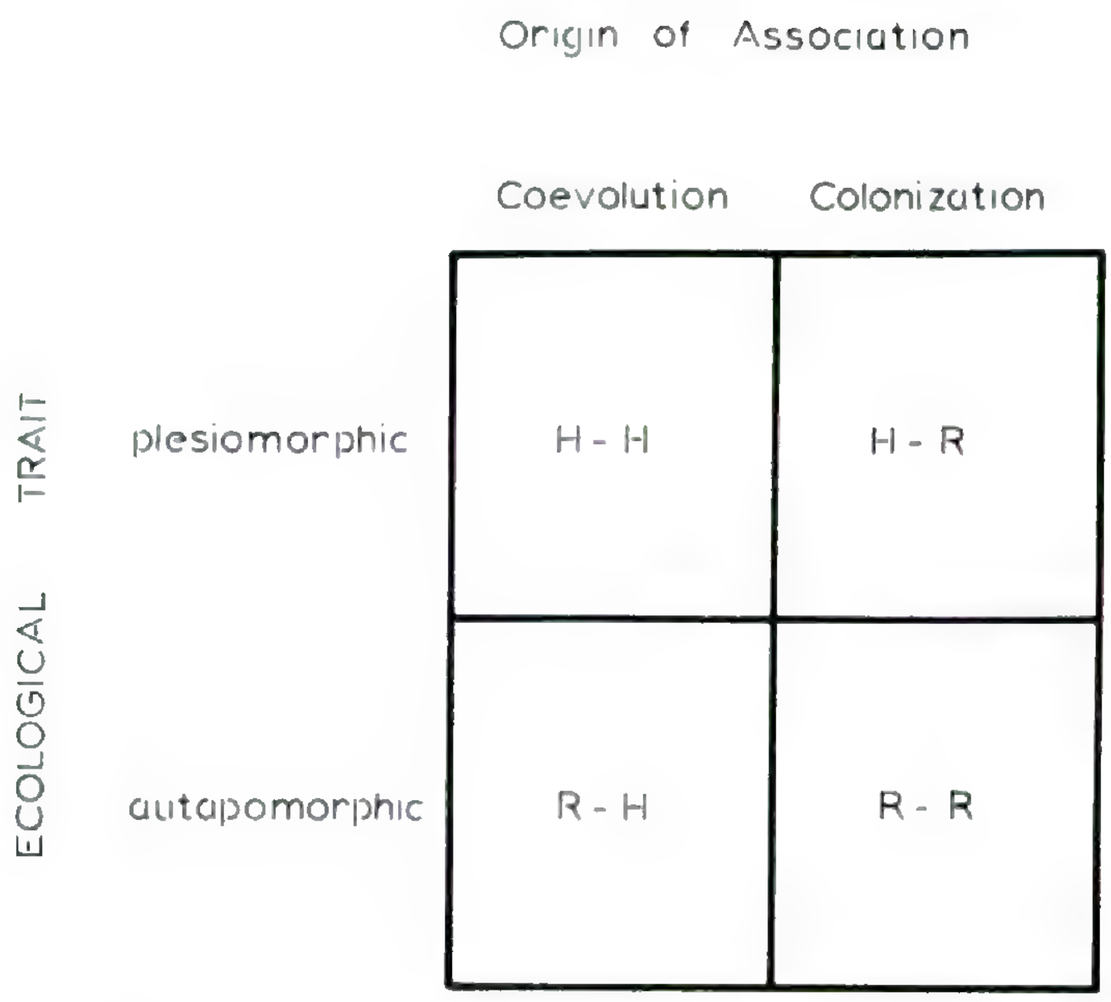


FIGURE 17. Two by two contingency table showing possible evolutionary explanations for observed ecological associates and individual ecological life history traits. H = historical, or inherited; R = recent, or modified in the given case.

first place (see also Ross, 1972b). Evolutionary ecology, by virtue of its reliance on indirect estimates of history, must rely on a form of uniformitarianism—if competition maintains traits today, it was responsible for their origin in the past.

Historical analysis also allows one to compare the relative degree of parallel (sometimes called adaptive) evolution exhibited by different groups. Parasites, for example, are supposed to be paradigms of adaptive radiations (Price, 1977, 1980). And yet, recent studies of various groups of parasitic worms (Brooks & Glen, 1982; Brooks et al., 1985a, 1985b) have documented consistency indices of 0.74 to 0.95, suggesting very low levels of parallel evolution.

Lastly, by preparing a cladogram for a given group of organisms based on non-ecological traits (i.e., structural rather than functional traits), then mapping ecological diversification onto the tree (Farris optimization: Farris, 1970), one can determine whether ecological diversification precedes or lags behind morphological diversification (see e.g., Ross, 1972a, 1972b; Resh et al., 1976; Morse & White, 1979). Such analyses can have startling effects. Brooks et al. (1985b) recently finished a family-level analysis of digenetic trematodes, based on 211 morphological characters. When all data for six different *categories* of ecological diversification were mapped onto the cladogram, only 26% of the tree was resolved. The historical picture is one of ecological diversification lagging behind morphological diversification. Ross (1972b) estimated that one ecological shift occurs for approximately 30 speciation events in phytophagous insects. Boucot (1983b) has suggested that this ecological conservatism is a general picture in the fossil record.

The applications of historical ecological analysis in this third area are just beginning. I will now present a case study to illustrate the kinds of applications I envision for historical ecology.

We may establish the topology of interactions for a given ecological association by direct observation. I have tried to show that it is possible to establish robust hypotheses of the relative recency of association among the members. By using those two types of data, it is possible to estimate the extent to which contemporary interactions are responsible for ecological life history traits. Species may occur together because they evolved together, vicariantly, or because at least one dispersed from its area of origin. Ecological life history traits exhibited by two or more interacting species may be traits inherited unchanged from ancestors or they may be traits that evolved concomitantly with the contemporary association. Figure 17 summarizes the four possible combinations of circumstances this provides.

For members of a vicariant association whose ecological interactions result from plesiomorphic (ancestral) ecological life history traits, their interactions may be completely explained by reference to historically determined properties of the organisms, namely, their inherited traits and their geographical history. There may also be associations in which at least one member has dispersed from its area of origin but for which interactions still result from expression of ple-

siomorphic ecological life history traits. For such associations only the contemporary ability of one (or more) of the species involved to disperse need be added to the historically determined traits to explain the observed interactions. For neither of these two classes of observations may contemporary ecological interactions be logically involved to explain the traits exhibited by the species involved.

The other two classes of observations are characterized by ecological life history traits unique to (evolving concomitantly with) a given contemporary association. Those traits may have arisen independently of ancestral interactions or may have arisen as a result of ancestral interactions. Only for the latter case can it be said that influences extrinsic to the organism, in this case the ecological interactions of other species, were responsible in any way for a particular set of traits that we observe today.

In many cases, it is possible for different equally-parsimonious interpretations of the ancestral condition to be postulated (Farris, 1970; Mickevich, 1982; Swofford & Maddison, unpubl. data). The examples that I will present next have been chosen so that they are relatively unambiguous, but research into the properties and assumptions of various optimization schemes for predicting ancestral traits is of utmost importance for applying this technique generally.

Holmes (1973) reported that the digeneans *Psettarium sebastodorum* and *Aporocotyle macfarlani,* inhabiting the circulatory system of rockfishes, exhibited little niche overlap. *Psettarium sebastodorum* occurs almost exclusively in the heart whereas *A. macfarlani* is almost entirely restricted to the blood vessels of the gill arches. Holmes assumed that parasite community structure is affected to a large degree by interspecific competition. From this, he concluded that the non-interactive site selection by the two species of blood flukes was de facto evidence of past competition.

Rohde (1979) examined the same data as Holmes. He assumed that natural selection could explain the observed differences in site selection easily. All one need do is invoke the notion that selection would favor flukes that clumped together in the host because they would have a higher probability of mating. His conclusions: one need not invoke competition to explain the observations. The data are evidence of the effectiveness of natural selection.

Price (1977, 1980) also examined Holmes' data.

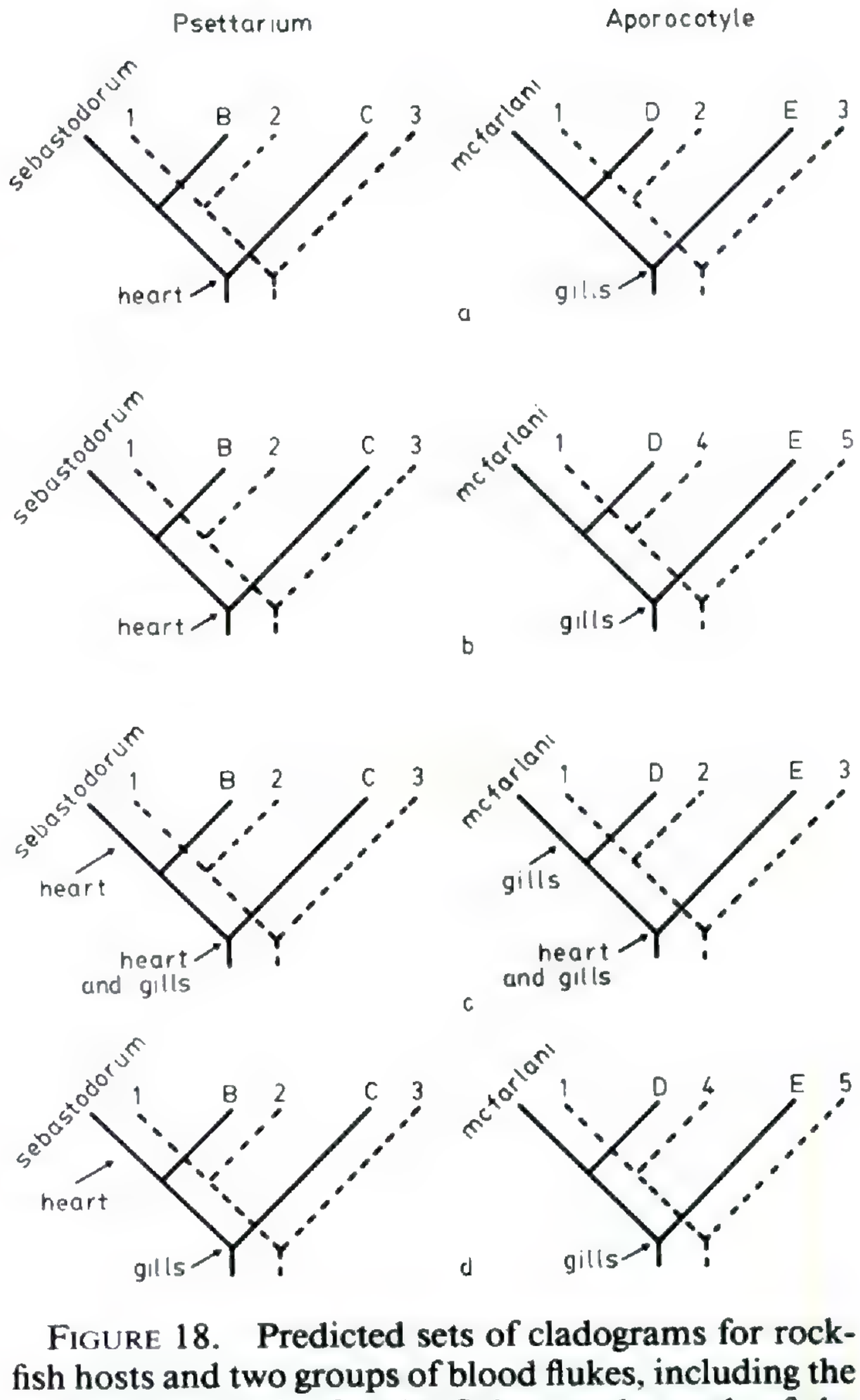


FIGURE 18. Predicted sets of cladograms for rockfish hosts and two groups of blood flukes, including the site selection traits for the flukes, under each of the four contingencies listed in Figure 17.—a. Historically determined association and traits.—b. Historically determined traits, recent (colonizing) association.—c. Historically determined association, recent (autapomorphic) traits.–d. Recent (colonizing) association and recent (autapomorphic) traits (redrawn from Brooks, 1980a).

His assumption was that parasite communities, because they are generally found to be below MacArthur-Wilson (MacArthur & Wilson, 1967) equilibrium, are never established and persistent for long periods but are always young colonizing communities. He further asserted that generalized parasites are young colonizers and specialized parasites are not. Given the two specialized parasites in a young colonizing community, Price concluded that the parasites were pre-adapted to their specialized niches and therefore colonized them. Competition and selection played minimal roles in their site selection in rockfish.

Finally, Brooks (1980a, 1980b) suggested that the parasites could be part of a coevolving fauna, that is, a vicariant ecological association, exhibiting plesiomorphic ecological life history traits

for site specificity (habitat loyalty). The four different opinions each correspond to one of the general classes listed in Figure 17 and are shown in Figure 18. Brooks (1980a, 1980b) suggested that each of the four explanations predicted an explicit set of phylogenetic relationships and shifts in characters and/or hosts.

For Brooks' contention to be correct, the two different parasites must exhibit a vicariant (= coevolving) relationship with the same host group and must exhibit plesiomorphic life history traits. Figure 18a summarizes those attributes. Price's hypothesis (Figure 18b) would not differ too greatly, except that either *Psettarium* or *Aporocotyle,* or both, would be colonizers in rockfish, so the host–parasite relationships indicated by each parasite group would differ. Rohde's hypothesis involves hosts and parasites that are together for a considerable period of time during which natural selection promotes progressively narrower site selection. This is shown in Figure 18c, where the parasites exhibit vicariant host relationships as well as autapomorphic ecological life history traits. Finally, we consider Holmes' hypothesis of competitive interactions mediating site selection (Fig. 18d). Corroboration of this class of hypotheses requires both elements of dispersal and the expression of autapomorphic traits relevant to the dispersal. Autapomorphic traits are features of the evolutionary context of the ecological interactions.

Holmes and Price (1980) attempted to analyze the *Psettarium/Aporocotyle*/rockfish system according to the above protocol. They concluded that there was no historically determined component in the interaction. Both species of parasites were deemed to be colonizers of rockfish and were "ecological specialists" in other hosts. Note that this corresponds to the situation found in Figure 18b, in which the ecological life-history traits exhibited are plesiomorphic, that is, historically constrained. Thus, Holmes and Price were incorrect in asserting that their conclusions supported strict ecological determinism. They also asserted that: ". . . the genealogies of parasites and their hosts are clearly not congruent (eliminating all four cases of Brooks' Figure 4)." Brooks' "Figure 4" refers to Figure 18. Note that for only Figure 18a and 18c are host and parasite genealogies congruent. Note also that Figure 18b corresponds to the conclusions Holmes and Price drew. Thus, they were also incorrect in saying that they had eliminated all four cases Brooks (1980a) proposed. These inconsistencies in their conclusions led me to re-examine Holmes and Price's phylogenetic hypotheses. Regarding *Psettarium,* they wrote: "The genealogy of three species of *Psettarium* is not clear (see differentiating characteristics in Holmes, 1971). However, it does not appear that *P. japonicum* and *P. tropicum* are more closely related to each other than to *P. sebastodorum.* The male terminal genitalia of *P. sebastodorum* are more similar to those of *P. japonicum* than to those of *P. tropicum,* suggesting the genealogy of figure 2B." Upon examining the primary literature, I found that the similarity in male terminal genitalia between *P. sebastodorum* and *P. japonicum* is based on their possession of a cirrus sac (a bag containing the male intromittent organ)—*P. tropicum* lacks a cirrus sac. However, the presence of a cirrus sac is plesiomorphic not just for fish blood flukes, but for all flukes. Therefore, its absence in *P. tropicum* is not indicative that *P. sebastodorum* and *P. japonicum* are each other's closest relatives. However, *P. tropicum* and *P. japonicum* are both wide-bodied, whereas *P. sebastodorum* is slender and elongate. In order to determine which trait might be plesiomorphic, we needed to examine close relatives (out-groups) of *Psettarium* spp. Manter (1954) had stated that the differences between *Psettarium* and the genus *Cardicola* were "not clear" and "seemed rather inadequate." Holmes (1971) stated: "These two genera [*Psettarium* and *Cardicola*] are very similar, and certainly do not belong to different subfamilies." Of the nine species of *Cardicola,* some are elongate and some have wide bodies. Finding no clearcut support within *Cardicola,* I then examined two other related species, namely, *Paracardicola hawaiiensis* and *Neoparacardicola nasonis.* Both of these species have two testes, the plesiomorphic condition for flukes. Members of *Cardicola* and *Psettarium* have only one testis; thus, they would seem to form a monophyletic group based on that trait. Both *P. hawaiiensis* and *N. nasonis* are elongate worms, suggesting that elongate bodies are plesiomorphic for the group. Thus, *Psettarium tropicum* and *P. japonicum* would be closest relatives based on sharing the apomorphic trait of wide bodies. *Psettarium* is supposed to be discrete from *Cardicola* by virtue of possessing a bend in the posterior margin of the body at the point of the male genital pore. However, *Neoparacardicola nasonis* exhibits that trait, making it either a convergent trait or a plesiomorphic trait among these flukes. Thus, *Psettarium* has no real support as a mono-

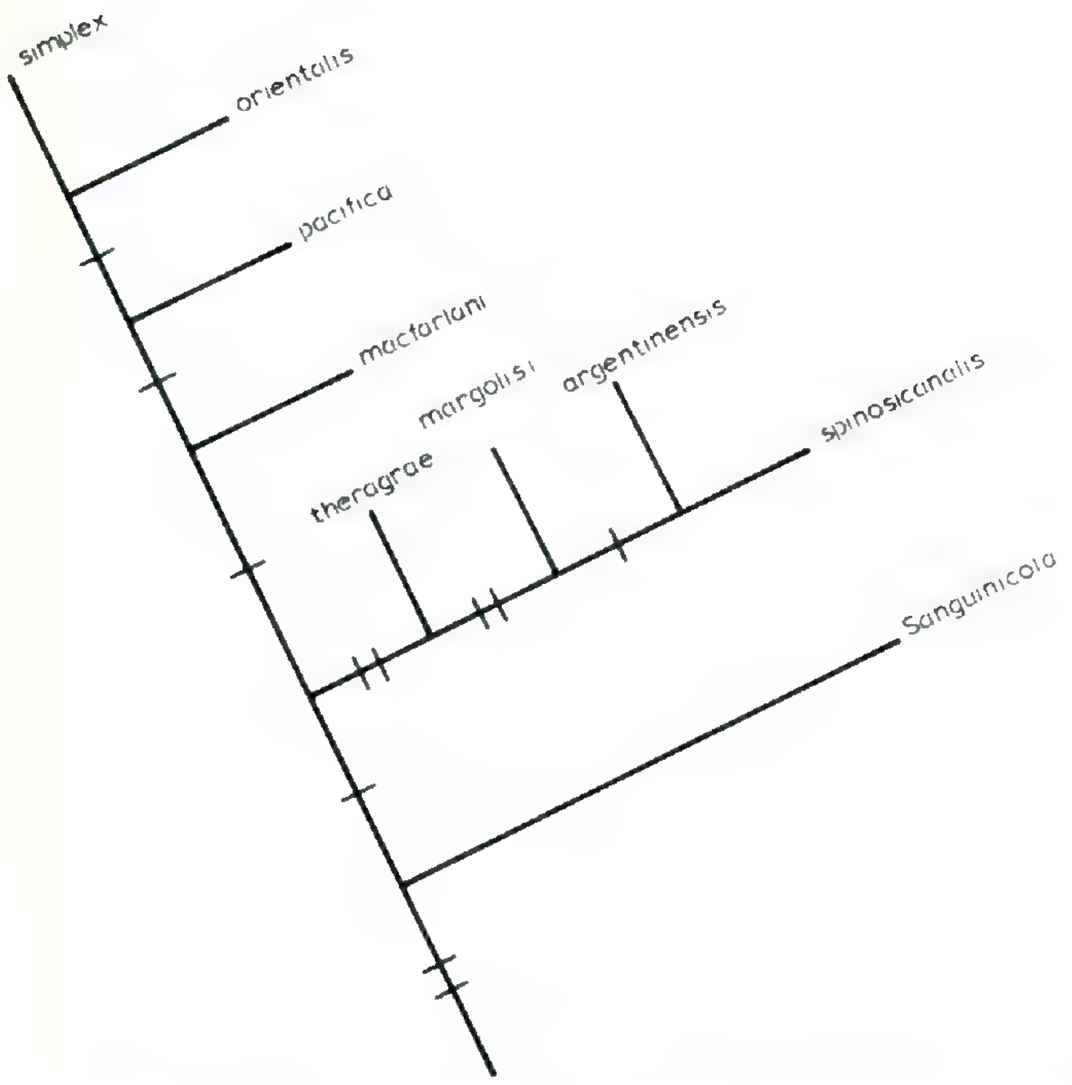
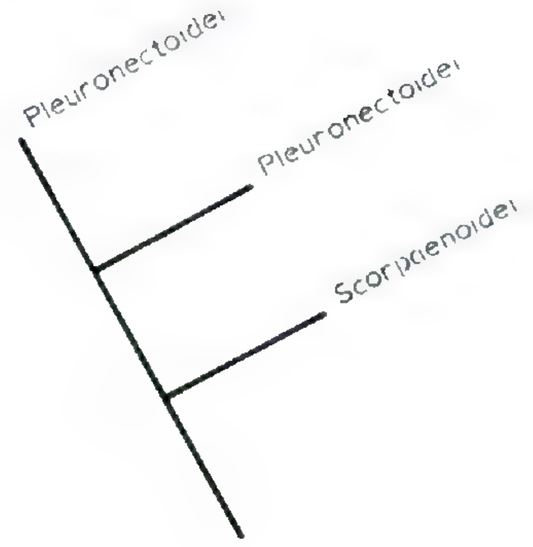


FIGURE 19. Cladogram depicting phylogenetic relationships of species of *Aporocotyle,* a genus of blood flukes inhabiting fish.



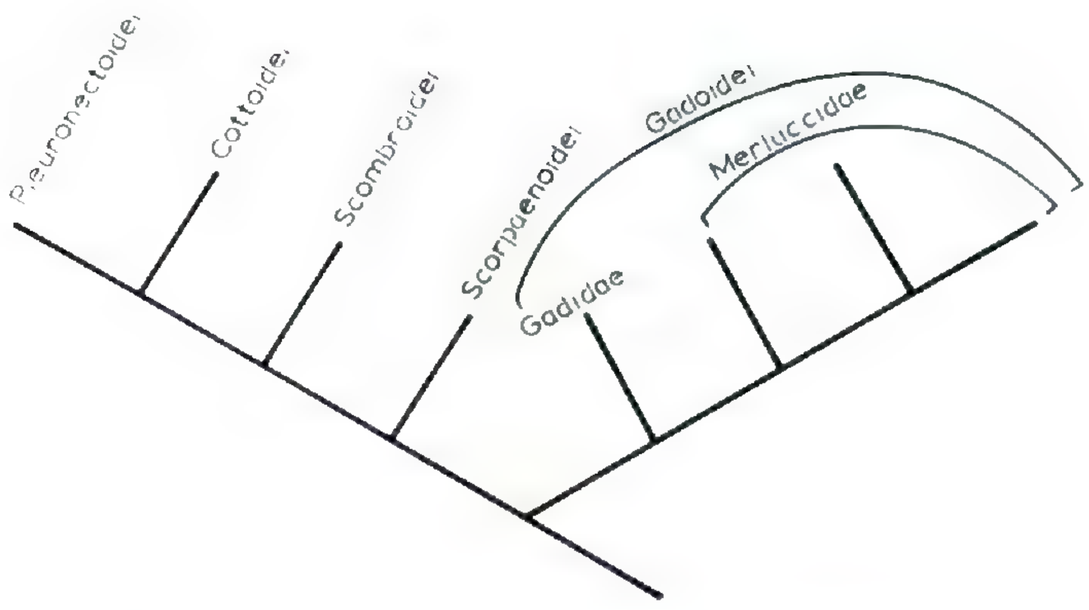


FIGURE 20. Host relationships indicated by phylogenetic relationships of *Psettarium* spp. (top) and *Aporocotyle* spp. (bottom).

phyletic group distinct from *Cardicola. Cardicola,* however, has been distinguished only because it lacks the body bend of *Psettarium*; thus, there is no character support for *Cardicola* as a real group either. I will return to this point later.

The genealogy for *Aporocotyle* presented by Holmes and Price (1980) suffers from similar analytical flaws. Much of their cladogram is based on presence or absence and arrangement of body spines and number of testes. All members of *Aporocotyle* have multiple testes, as do members of their closest relative, *Sanguinicola.* However, as mentioned before, the plesiomorphic number of testes in flukes is two. Holmes and Price's genealogy of *Aporocotyle* arranges species beginning with those having more than 130 testes and terminating with those having 25–32 testes. Outgroup comparisons would support a reversal of that trend. In addition, enlarged lateral body spines are used as indicators of relationships among species of *Aporocotyle,* even though *Sanguinicola* spp. have them as well. Figure 19 depicts the phylogenetic hypothesis best supported by those characters re-interpreted in strictly phylogenetic terms.

In Figure 20, the cladogram for *Aporocotyle* and one for the three *Psettarium* species are displayed, with their host groups superimposed in place of species names. Although there is not much resolution, there is no evidence supporting host-switching. The possible vicariant association between the two groups of blood flukes and the various host groups could be better examined if species of *Psettarium* occurred in cottoids or scombroids. Interestingly, four species of *Cardicola* occur in cottoids and three in scombroids. At least one of those occurring in cottoids, *C. laruei,* has a wide body like *P. japonicum* and *P. tropicum.* [The remaining two species of *Cardicola* inhabit mugiloid and labroid fishes, respectively.] Figure 21 shows Figure 20a redrawn to include the species of *Cardicola*; Figure 22 shows the relative relationships of the fish groups involved and their associated blood flukes.

The new analysis demonstrates no incongruence among the host and parasite cladograms (Fig. 23). However, the vast majority of species of fish in each of the host groups have no blood flukes reported from them. This suggests that (sampling error aside) although both groups of blood flukes have coevolved with their hosts, that coevolution has been marked by independent failure of the two groups of flukes to persist in all evolving host lineages. The absence of parasites from many hosts does not indicate the degree of relationship among those that survive. It is not inconsistent with coevolution that in only one known case do members of *Aporocotyle* and

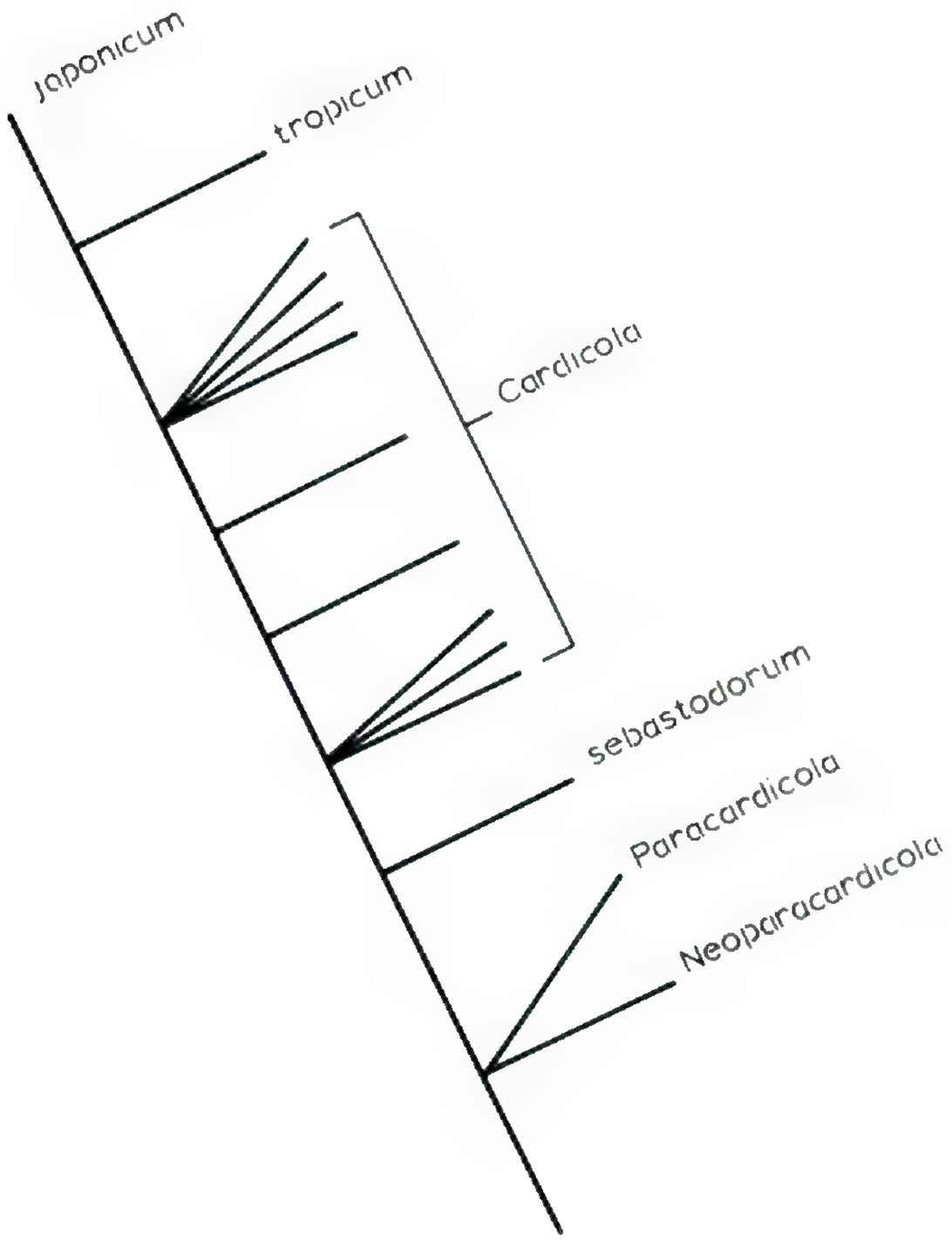


FIGURE 21. Phylogenetic relationships of *Psettarium* spp. (*P. japonicum, P. tropicum, P. sebastodorum*), *Cardicola* spp., and two outgroups (*Paracardicola* and *Neoparacardicola*). Note that *Psettarium* is polyphyletic and *Cardicola* is paraphyletic.

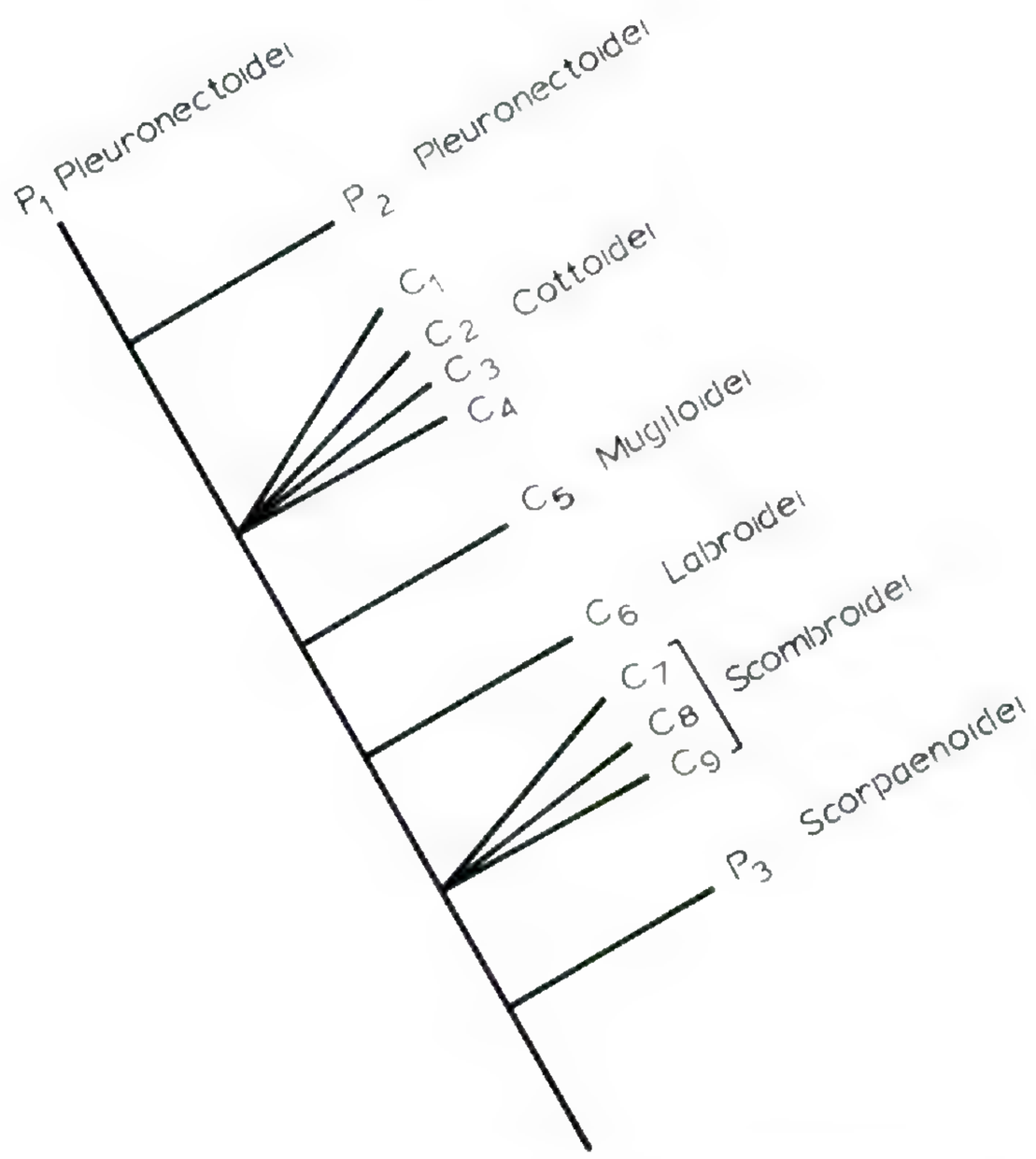


FIGURE 22. Host relationships indicated by phylogenetic relationships of *Psettarium/Cardicola* spp.

Psettarium-Cardicola occur in the same host. This is especially true if the hosts in which the co-occurrence happens are relatively primitive, as they are in this case.

Having established the temporal context of the association between *Aporocotyle macfarlani, Psettarium sebastodorum,* and *Sebastes* spp., we may now examine the possibility of interactive or non-interactive factors determining the site-selection exhibited by the parasites. For this we take the two parasite cladograms and superimpose their habitat site rather than the species names at the ends of the branches. We then estimate the ancestral conditions by means of "Farris optimization" (see Kluge & Farris, 1969; Farris, 1970) (Figs. 24, 25). Having those data, we may see that *A. macfarlani* occurs in the gills because its ancestor was a gill-inhabiting parasite but *P. sebastodorum* is most likely descended from a species that inhabited the mesenteric blood vessels. Thus, *P. sebastodorum* exhibits an autapomorphic trait for site selection. This would appear to support Rohde's hypothesis, for that species at least. However, no other species in the group shows a similar tendency. The shift in traits

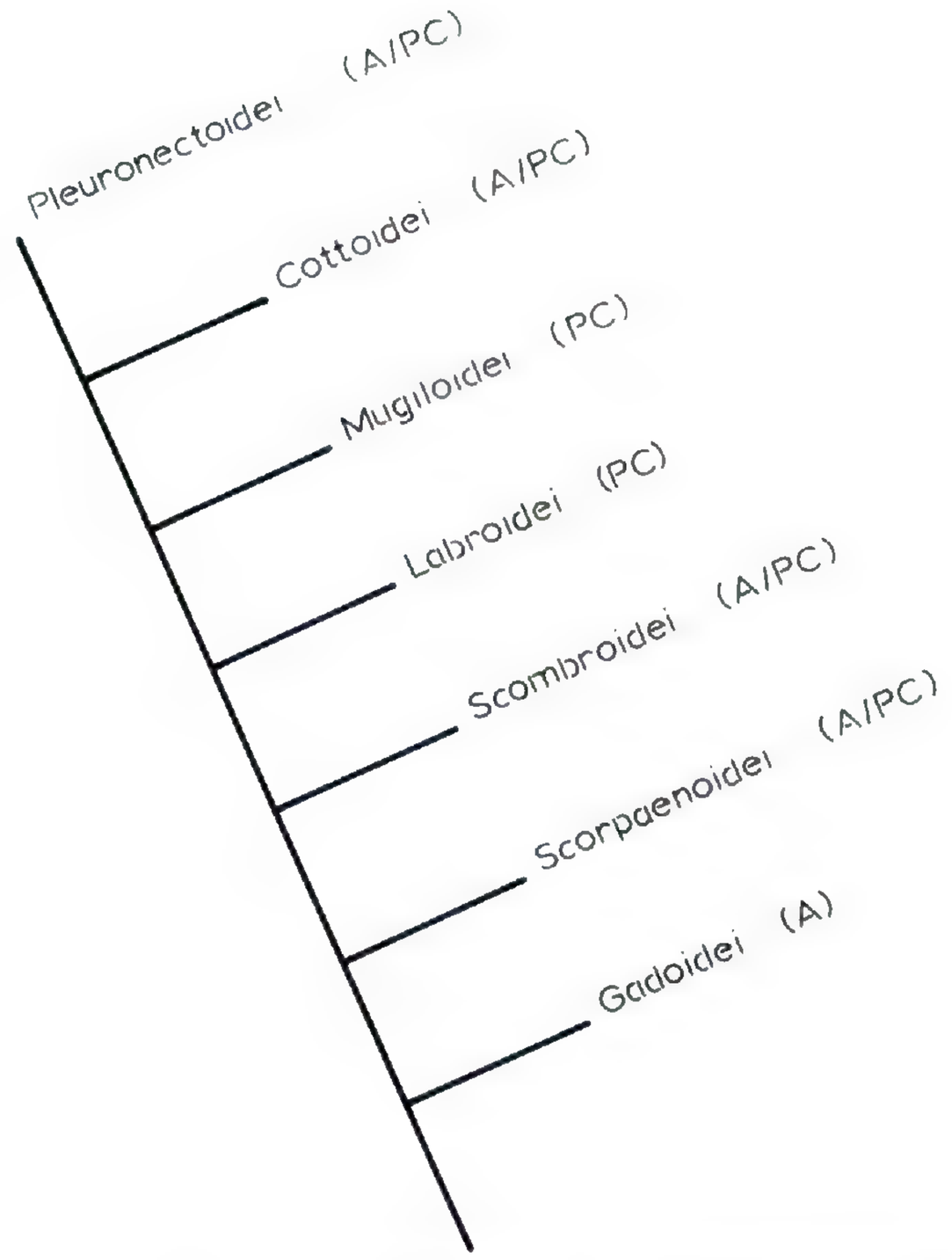


FIGURE 23. Summary set of host relationships supported by both *Aporocotyle* spp. (A) and *Psettarium/Cardicola* spp. (PC). Note congruence.

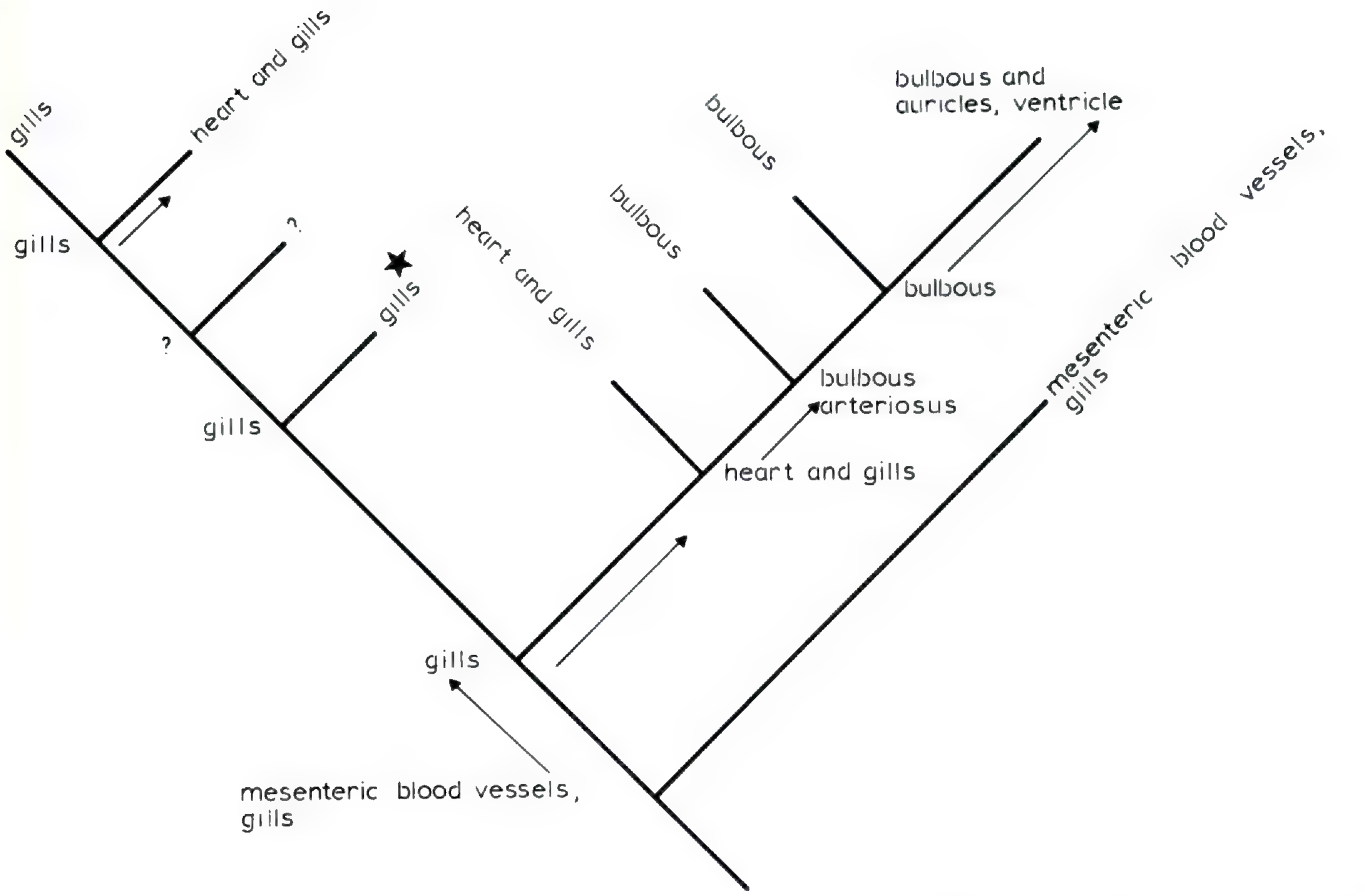


FIGURE 24. Summary of site selection traits for species of *Aporocotyle*. Arrows indicate required evolutionary changes; question mark indicates unknown data; star indicates *A. macfarlani*.

would not seem to be explicable in terms of competitive exclusion, because *A. macfarlani* does not occur in the mesenteric blood vessels. The change in site by *P. sebastodorum* does not seem to be correlated with an extrinsic variable, so we conclude that the structure of this ecological association is historically determined. This contrasts with the South American freshwater stingray parasite associations that include some colonizers.

It is important to emphasize that historical evidence for adaptive changes of the type sought by evolutionary ecologists appear as exceptions to the historical pattern of structural and functional traits. Adaptive shifts are manifested by the same, or highly similar, traits arising in species that are not each other's closest relatives, but that share common ecological regime, in which the convergent traits are correlated with that particular ecological regime. In asking the question, "How often do such shifts occur?," Ross (1972b) concluded that for a survey of various insect groups the answer was 1–20%, with an average of about 3% (one in every 30 speciation events). This accords well with my studies of parasitic helminths. If this is generally true, there does not

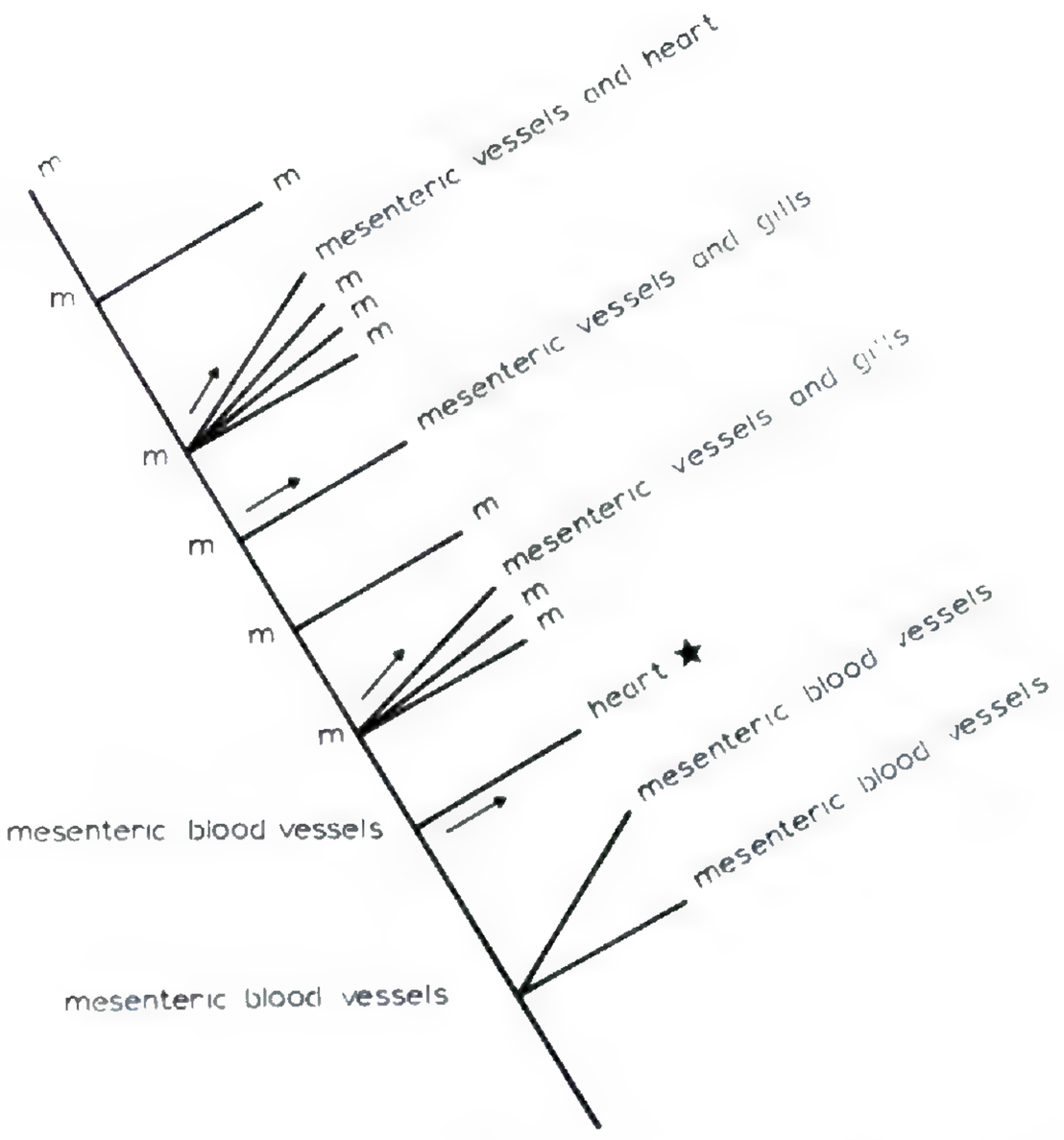


FIGURE 25. Summary of site selection traits for species of *Psettarium/Cardicola*. Arrows indicate required evolutionary changes; star indicates *P. sebastodorum*.

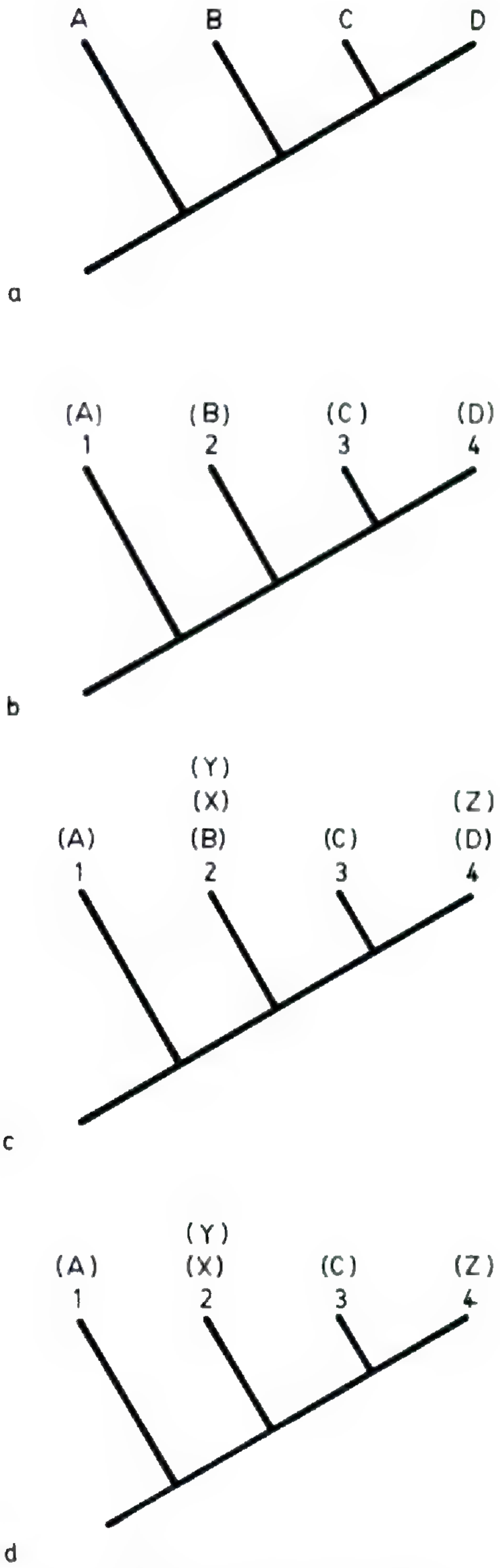


FIGURE 26. Demonstration that degree of co-accommodation (host specificity) need not be great in order for the method proposed in this study to detect historical patterns.—a. Depicts a host taxon's phylogenetic relationships.—b. Shows that the parasite taxon 1-2-3-4 has co-speciated with the host taxon.—c. Depicts broadening co-accommodation by some members of the parasite taxon; note that co-speciation of ABCD and 1-2-3-4 can still be discerned.—d. Depicts the host–parasite relationships of parasite taxon 1-2-3-4 if B and D are no longer host members of the parasite taxon. In this case, even though a number of unrelated hosts are used, the historical pattern is still present (redrawn from Brooks, 1981b).

seem to have been enough ecological diversification to explain evolutionary diversification.

If historical constraints play a major role in determining ecological structure, we would expect to find evidence of them at higher systematic levels than the species. As mentioned before, Brooks et al. (1985b) recently presented a phylogenetic analysis of the 62 families of digeneans (to which *Psettarium, Cardicola* and *Aporocotyle* belong). Only 26% of the groupings and 35% of all branches on the phylogenetic tree were characterized by ecological changes. Classes of ecological traits considered were: (1) changes in developmental programs producing increased numbers of infective larvae, (2) changes in encystment behavior of infective larvae, (3) shifts in first host, (4) acquisition of and shifts in second hosts, (5) shifts in final host, and (6) changes in site of infection in the final host. Ecological changes definitely lagged behind morphological changes. Trends seen in species-level analyses are found in family-level analyses as well, attesting to the influence of historical constraints on ecological diversification.

SUMMARY

Historical ecology provides a missing component in studies of the evolution of ecological associations—history. This may seem like a strange assertion, since it is certainly true that evolutionary ecologists are vitally interested in historical phenomena. I think two perceptions have led to the exclusion of historical components in evolutionary ecology. The first is the perception that there exists no protocol for producing direct estimates of history that has any degree of empirical rigor. I hope that my few examples and the rest of the contributions in this volume provide reason for optimism that such a protocol is now firmly entrenched. The second perception goes something like this: even if we could provide direct estimates of history, the indirect measures we use now give us the same answers. Historical ecology allows us to investigate this perception.

In the past, I have examined three components of the evolutionary ecology of host–parasite systems: (1) "equilibrium" numbers of species, (2) host specificity, and (3) "resource-tracking" models (see Brooks, 1979b, 1980a, 1980b, 1981b). Consider the following possibilities derived from historical analysis. Suppose we discover an association that is very old and historically structured, such as the Parana River system stingray parasite fauna, and yet that association exists below predicted "equilibrium" numbers. Price (1980) noted that parasite communities

generally exist below equilibrium numbers and used that observation as evidence that parasite community structure reflects young, colonizing phenomena. From the historical perspective, it seems that the notion of "equilibrium" numbers of species may be an artifact of one theory of community evolution rather than empirical necessity.

Now let us consider the question of host specificity from the historical perspective. I have suggested previously that degree of host specificity is decoupled from historical association of lineages. Figure 26 provides an example of this. Notice that no matter what differences exist in degree of host specificity, the history of the parasite lineage is still coordinate with that of the original host lineage. Conversely, it is not necessarily true that very pronounced (host) specificity indicates a long-standing association. Finally, a related concept is that of "resource tracking" models of coevolution (see e.g., Kethley & Johnston, 1975). Resource-tracking models imply a set of specific historical predictions that are seldom, if ever, acknowledged. Chief among these is the assertion that not only do ancestors always persist, ancestors are always among the known species at any given time (see Brooks, 1981b for a fuller discussion). Thus, it seems that it is not true that the indirect estimates of history will always provide the same answers as explanations derived from direct estimates of history. Hence my assertion, at the beginning of this review, that historical ecology provides a complementary approach with evolutionary ecology to attaining insights into causal mechanisms of the evolution of ecological associations. Certainly the most interesting questions will involve cases in which the two approaches give different answers.

Finally, I would like to comment on the view, from historical ecology, of the current enthusiastic exchanges among ecologists concerning the relative merits of "competition" or "random association" null hypotheses in explaining the structure, or organization, of communities (see Lewin, 1983a, 1983b for a review). To do so, we must first represent the question in historical terms, then produce maximum randomness and minimum randomness configurations. I tried to show how to represent such questions in historical terms using the fish blood fluke example. A convenient measure of the relative randomness of an association of species and their ecological life history traits is the statistical entropy of the community ensemble. Using the method pioneered by Karreman (1955) and modified for use in examining phylogenetic questions (Wiley & Brooks, 1983), it is possible to show that the minimum randomness configuration is the one that is wholly determined historically. It is also possible to show that maximum randomness is not achieved by a random assemblage of species with fixed traits, but by the assemblage (random or not) of species with unlimited polymorphism for ecological traits; in other words the maximum randomness null hypothesis is indistinguishable from a maximum competition model when viewed historically. Somewhere in between lie all systems experiencing some competitive interactions. All of these are relatively more random than historically determined ecological associations. Thus, from the perspective of historical ecology, it is difficult to understand the hypothesis that competition is an organizing force in evolution. Accounting for such differences in perspective should provide exciting research projects in the future.

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PHYLOGENETIC PATTERNS AND HYBRIDIZATION[1]

V. A. FUNK[2]

ABSTRACT

Hybridization is an important part of the evolutionary history of flowering plants. If hybridization has occurred among the species of a taxon under cladistic analysis the results are varied but always present additional difficulties. Hybridization results in incongruent intersecting data that obscure the underlying hierarchy. Guidelines and methods are examined for their usefulness in identifying possible hybrids in a cladistic study. Seven genera are analyzed cladistically and the resulting cladograms examined for possible hybrids. These hypotheses of hybridization are then compared to other data, such as distribution and cytology, to see if the hypotheses of hybridization are supported or rejected. The more hybrids an analysis contains and the more complex the interactions, the more difficult it becomes to identify possible hybrids and their parents.

It is difficult to overemphasize the importance of hybridization and polyploidy in evolution because they are outstanding features of many plant groups. According to some authorities 30–80% of the species of angiosperms are polyploids (Goldblatt, 1979; Lewis, 1979; Stebbins, 1974), which allows for the possibility of a tremendous amount of hybridization. Of course, these figures do not include diploid hybrids. Despite its importance, hybridization has been virtually ignored by those who have dominated the discussion of evolutionary theory. This is a result, no doubt, of evolutionary theory being largely in the hands of scientists who work on groups in which such phenomena as polyploidy and hybridization have a strong relationship with unisexuality and are not considered important in evolution.

There are different types of hybridization. Figure 1 summarizes some of the possibilities (a more detailed explanation is found in Funk, 1981) but does not include introgression. For the purpose of this paper it is important to note that many hybrids are sexually reproducing individuals and are morphologically distinct and in some manner reproductively isolated from both parents. Thus, they behave as species no matter whose definition you chose to adopt.

THE STUDY OF HYBRIDIZATION

The basic concept of phylogenetic systematics (sensu Hennig, 1966) is an ever branching pattern or hierarchy. The method of cladistics (phylogenetic systematics) seeks to discover these patterns by grouping together taxa that share apomorphies (evolutionarily novel, unique, or derived characters). Hybridization, or reticulate evolution, is inconsistent with a method designed to depict hierarchies. Hybridization is, therefore, a cause of incongruent, intersecting data that obscure phylogenetic information. Cladists have been concerned with this problem for several years. Most realize that any method that seeks to identify patterns of relationship must be able to accommodate hybridization because of its frequency. Workers in the problems of hybridization and phylogenetic systematics include Bremer (1983), Bremer and Wanntorp (1977), Clark (1982), Funk (1981), Humphries (1983), Humphries and Funk (1984), Nelson (1983), Nelson and Platnick (1980), Rosen (1979), Wagner (1969, 1983), Wanntorp (1983), and Wiley and Brooks (1982).

One favorite method of botanists in estimating the closeness of relationships among taxa is the percentage of hybridization in crossing studies. An important point about such hybridization studies was made by Rosen (1979: 277): "reproductive compatibility is a primitive attribute for the members of a lineage and has, therefore, no power to specify relationships within a genealogical framework." We cannot use the ability of two or more species to hybridize as an indication of close relationship because the ability is rela-

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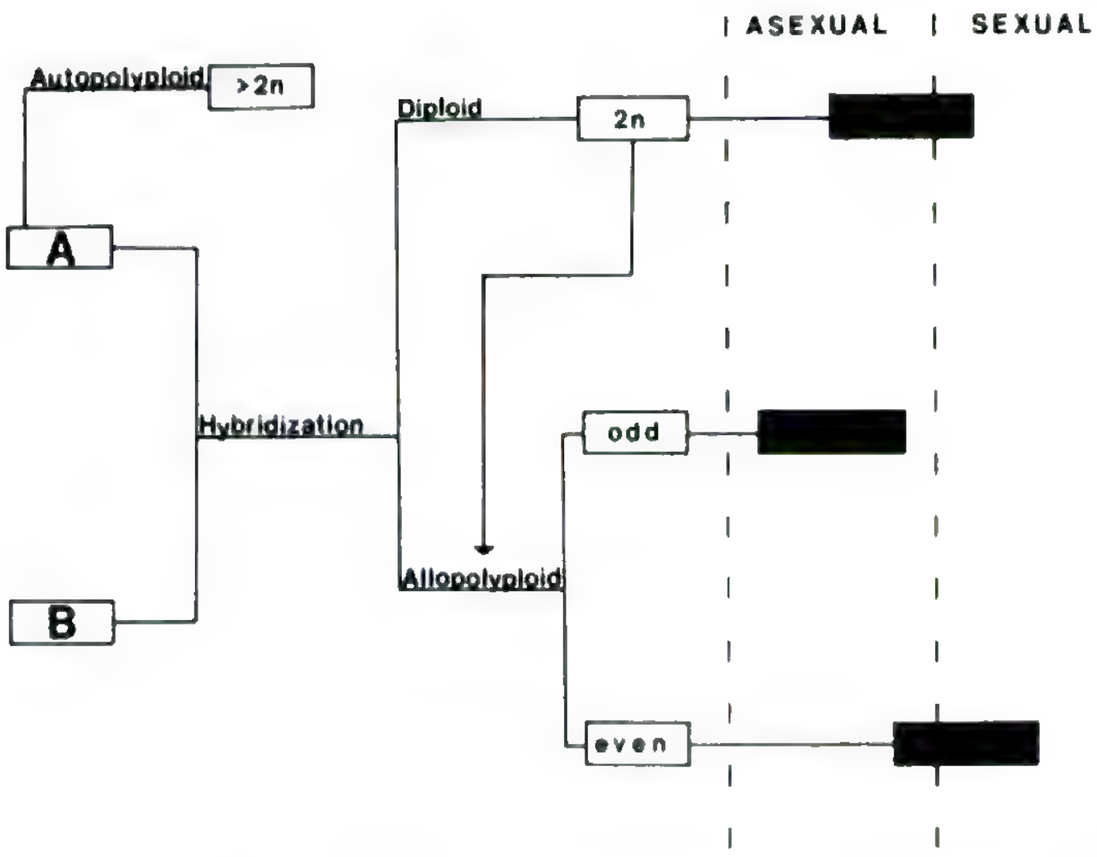


FIGURE 1. Possible hybrid and polyploid relationships of two species (A and B) and their reproductive capabilities (Funk, 1981).

tively ancestral, possessed at one time by all members of the group. In fact, it is the loss of the ability to hybridize that is apomorphic. Because it is never certain that any two taxa are unable to reproduce, whether or not species hybridize is uninformative in determining the pattern of relationship.

Among cladists, three different approaches have been suggested for dealing with the problem of hybridization (Humphries & Funk, 1984). Some suggest using the most parsimonious cladogram(s) and leaving the homoplasies (characters appearing more than once on the cladogram) resulting from the presence of hybrids as the true reflection of the character pattern. Others have advocated removing the hybrids that have been identified by their 'intermediacy' at the beginning of the analysis. The third group advises leaving all of the taxa in the analysis and then closely examining the cladograms for polytomies (nodes with more than two branches) and character conflicts that may indicate possible hybrids. There are problems with all three approaches. The first does not accurately reflect the character pattern; as we shall see, hybrids may appear on the cladogram in a polytomy or with character conflicts or even as ancestors when they are none of these. The patterns do not reflect the accurate sister-group relationship (nor are they true representations of phylogeny). The second approach assumes one can identify the hybrids prior to the analysis and this is not possible in many cases. The third position relies to a great extent on hybrids causing polytomies. Further analysis has shown this usually does not happen (Humphries, 1983).

Wagner (1983) has suggested a method for dealing with hybrids that he calls reticulistics. This method works with groups in which hybrids are intermediate in character and progressively less well with those that are not intermediate. Often the hybrids to which Wagner refers are F_1's that are being formed continually and are sexually inviable. Certainly for well-defined plant groups in which the hybrids are intermediate and obvious and are characterized by being rare and either sterile or polyploids (definition, Wagner, 1983: 71), Wagner's method should be considered. These individuals are not units of evolution and thus are not species. In this paper I am concerned with hybrids that are regarded as evolutionary units and that are usually designated as species, subspecies, or varieties.

Theoretically, in cladograms, hybrids show up by causing character conflicts; so also do homoplasies (Fig. 2, character 4; Appendix A). One must be diligent in trying to distinguish between character conflicts caused by hybridization and those that are the result of parallel or convergent evolution. It is advisable to use the cladogram (developed with the concept of parsimony using all taxa) to examine the apomorphies that appear more than once on the cladogram (homoplasies). Perhaps a closer examination will reveal that some characters originally thought to be apomorphies are actually different structures (false homologies) or are combinations of characters. For instance, not all black anthers in the Compositae genus *Montanoa* Cerv. are homologous. Although originally treated as one apomorphy (Funk, 1982) a close examination showed that some black anthers were black only around the edges of the thecae, some were black only on the top of the connective, while others were completely black. This additional information indicated that "black anthers" was not a single apomorphy but three apomorphies. Character conflicts can also be the result of a designated apomorphy actually containing several characters. Characters such as habit, chromosome number, and flower regularity, all can be divided into several characters. New apomorphies can be added to the cladistic study to reflect the additional information because the "groups of characters" should not be viewed as character conflicts but rather as separate apomorphies. Such changes should be made only when available evidence indicates that they are not homologous. Remaining character conflicts are the result of either undetected homoplasy or hybridization.

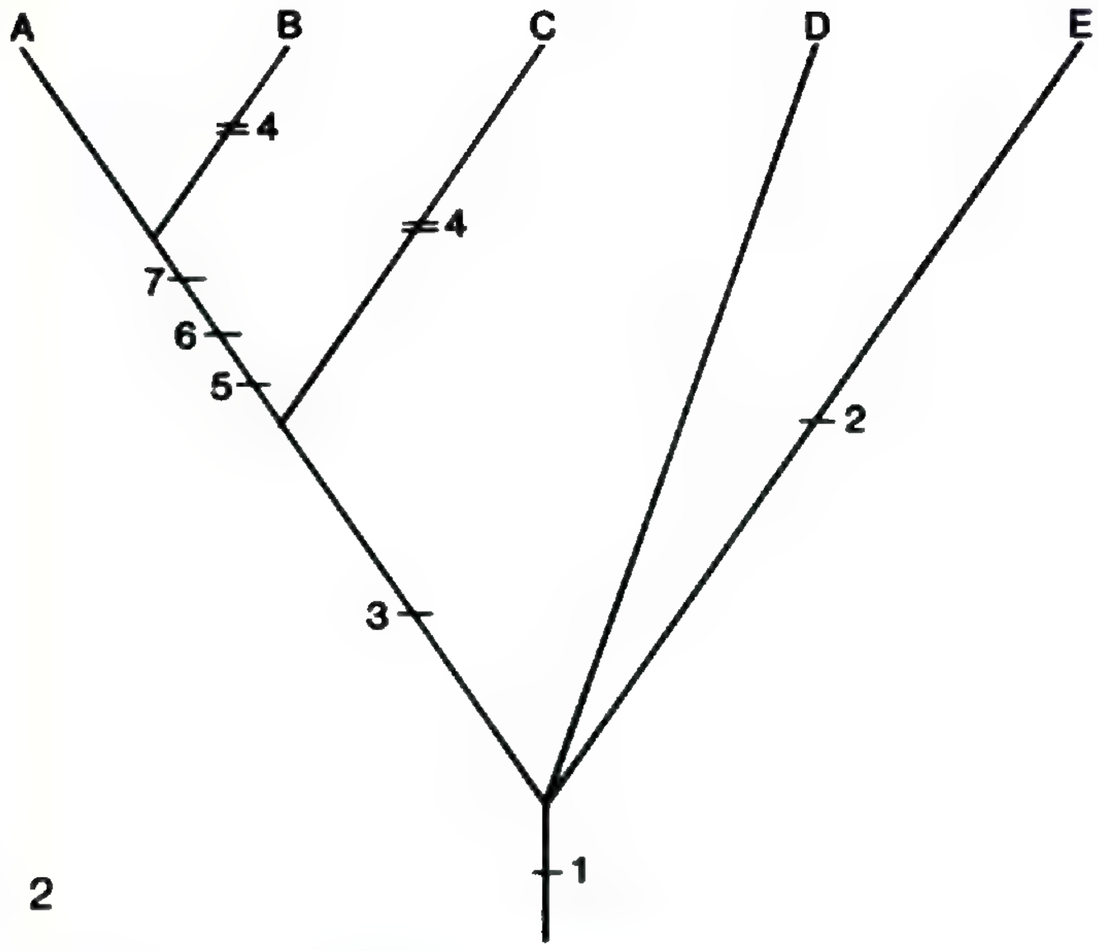
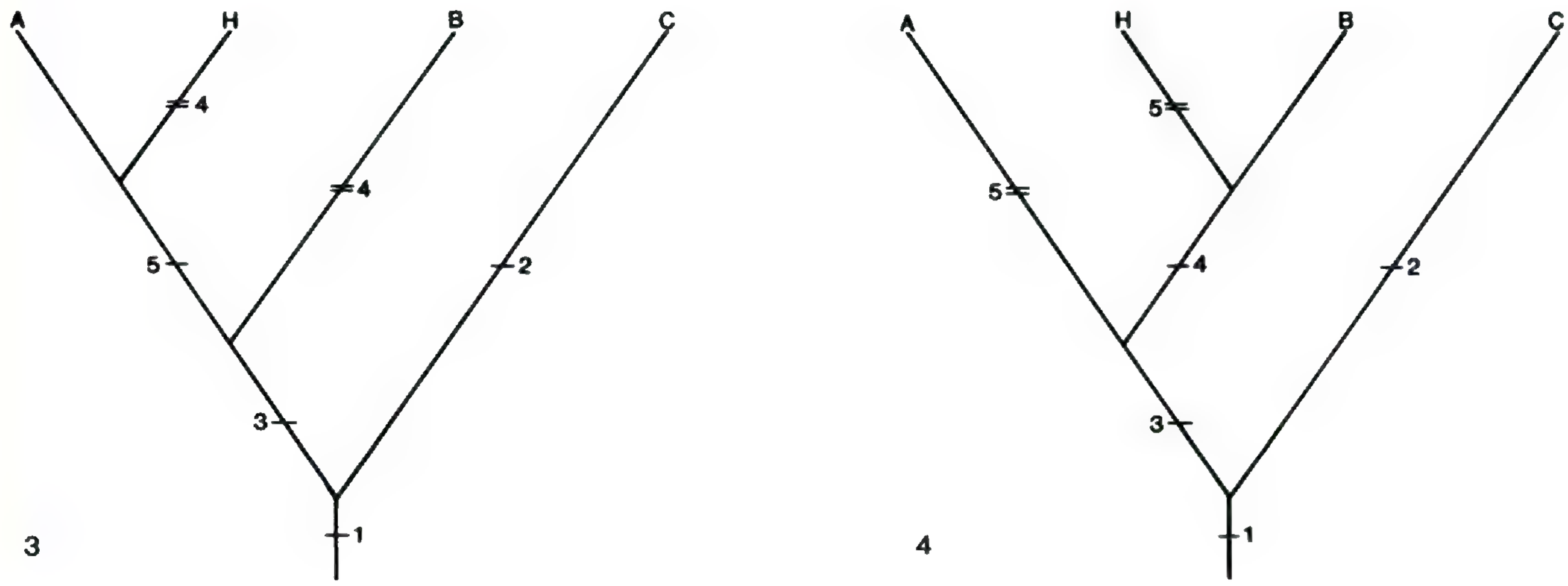


FIGURE 2. Cladogram illustrating character conflict that can be the result of either hybridization or parallel evolution.

A lack of apomorphies can also be caused by hybridity. The hybrid does not necessarily inherit all of the apomorphies of both parents. This observation is important: there is no reason to assume that all apomorphies are dominant over the more plesiomorphic characters of a transformation series. The data presented later in this paper indicate that in the heterozygous condition of the hybrid there might well be a higher percentage of plesiomorphic characters showing in the phenotype. Therefore, it is possible for the hybrid to show only plesiomorphies (primitive, ancestral, or more general characters) and appear on the cladogram in an ancestral position. In Figure 2, taxon D could be a hybrid, between taxon C and any other taxon, that inherited the plesiomorphies of both parents. Indeed, it is interesting to speculate on whether or not one could use such cladistic studies to identify interesting genetic problems.

Often the hybrids in a cladistic analysis will be grouped with one or the other of the parents depending on with which parent they share the most apomorphies (Humphries & Funk, 1984). When the putative parents are sister species (two species that are more closely related to one another than they are to any other species), hy-



FIGURES 3–6. Cladograms illustrating the pattern of species A and B and their hybrid, H.

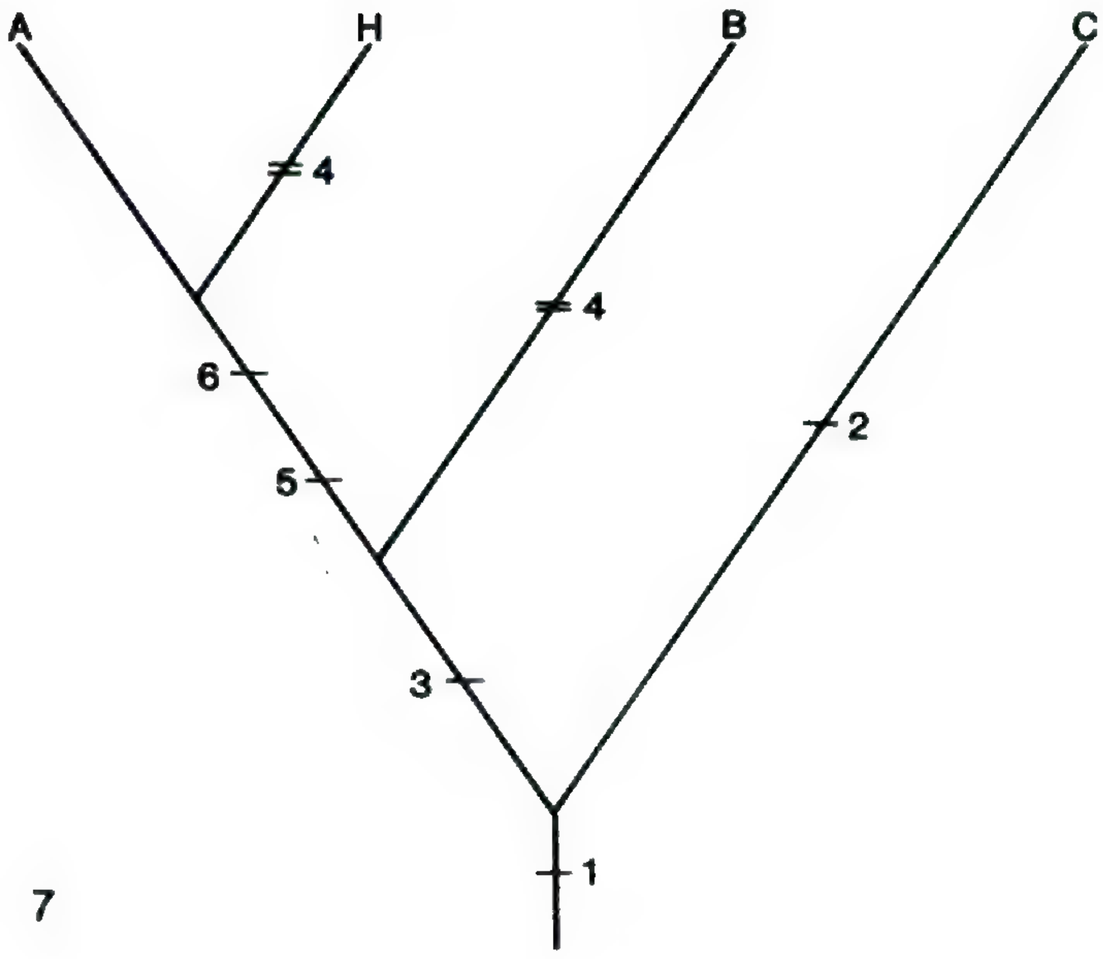


FIGURE 7. Cladogram illustrating the pattern of species A and B and their hybrid, H.

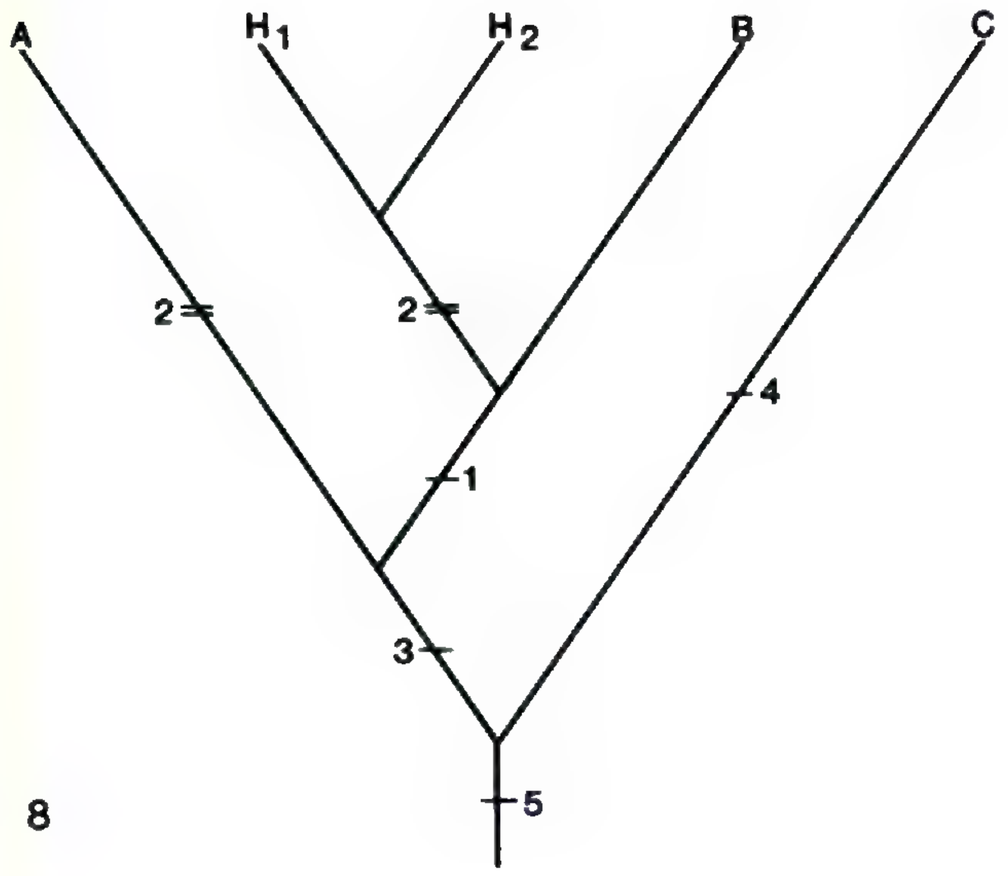
brids are quite often apparent regardless of whether or not they form polytomies. Hybrids that form dichotomous branching patterns can be identified as such so long as they have at least one apomorphy of both parents or if they lack an autapomorphy of the parent with which they are grouped. For instance in Figures 3–5 (for characters see Appendix B), species A and B hybridize to give species H. If there were an equal number of apomorphies in A and B (characters 4 and 5) and if both were found in the hybrid, the result could be expressed as two equally parsimonious cladograms (Figs. 3, 4) or as a trichotomy (Fig. 5), although the latter involves one more character change and is therefore one step longer. If the incongruent character set is inferred to be the result of hybridization, the hybrid could be placed above the diagram connecting with both parents (Fig. 6). However, if one parent taxon had one more autapomorphy than the other, or if the hybrid showed unequal character inheritance, then a single cladogram results. For instance, if taxon A (Fig. 7; Appendix C) had two autapomorphies (5 and 6), and the hybrid inherited all apomorphies of both parents, the most parsimonious cladogram would give the result shown in Figure 7. Nonetheless, because they are sister taxa, the possibility of hybridization is apparent, so long as the hybrid has at least one apomorphy from each parent. However, as mentioned earlier it is possible for the hybrid not to display all the apomorphies. If the hybrid in Figure 7 did not have character 4 there would be no indication that it was a hybrid (except for the more indirect evidence of lack of apomorphies in taxa A and H). If one parent has very few autapomorphies there is less chance that the hybrid will have any indication of its history.

Sometimes there is more than one hybrid from the same two parents (Figs. 8–12; Appendix D). The two hybrids are most parsimoniously grouped with either parent (Figs. 8, 9) but the two equally parsimonious cladograms indicate the hybridity of H1 and H2. The most parsimonious cladogram has two reticulations (Fig. 12). It is, of course, possible that taxa H1 and H2 are the result of a single hybridization event followed by segregation. One way to evaluate this possibility is to examine the distribution of the taxa in question. The possibility of hybridization followed by segregation lessens as the distance between the hybrid taxa increases.

The only time it is "most parsimonious" to have a polytomy is when the hybrid does not have any of the autapomorphies of either parent (Fig. 13; Appendix E).

However, parent taxa are not always sister taxa. For instance, Wagner (1954) has shown that at least three diploids are involved in producing the hybrids in *Asplenium,* and Grant (1953, 1964) has shown that species from different species groups are hybridizing in *Gilia* (Funk, 1981). In cases such as this the task of identifying hybrids becomes more difficult. For instance, given the cladogram in Figure 14 (Figs. 14–17, 19; Appendix F) the most parsimonious cladogram that includes the hybrid, places the hybrid (H, Fig. 15) as the sister taxon of the parent that involved the least number of homoplasious events (the number of character changes or length of this cladogram is L = 11). The length would increase if the hybrid were grouped with the other parent (Fig. 16, L = 12) because there is one more homoplasy. It is much longer to form a polytomy (Fig. 17, L = 14). The only time a polytomy would be formed in the most parsimonious cladogram is if the hybrid had none of the apomorphies of either parent, at least those above the first node shared by both parents (Fig. 18; Appendix G). If the hybrid is identified as such it can be removed from the cladogram and placed above it giving an even shorter cladogram (Fig. 19, L = 9).

The identification of possible hybrids is only the beginning of an analysis. Those cladograms indicating hybrids (e.g., Fig. 19) are merely hypotheses of hybridization and should be tested by using other data, such as distribution, chro-



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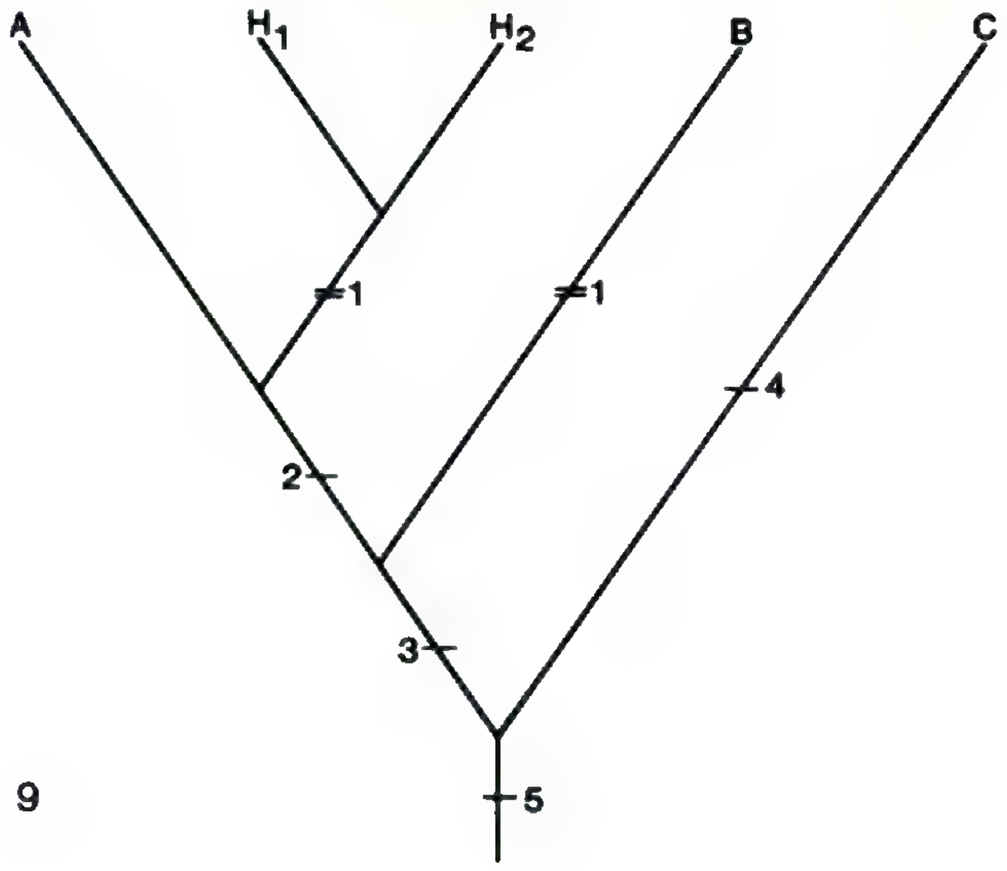

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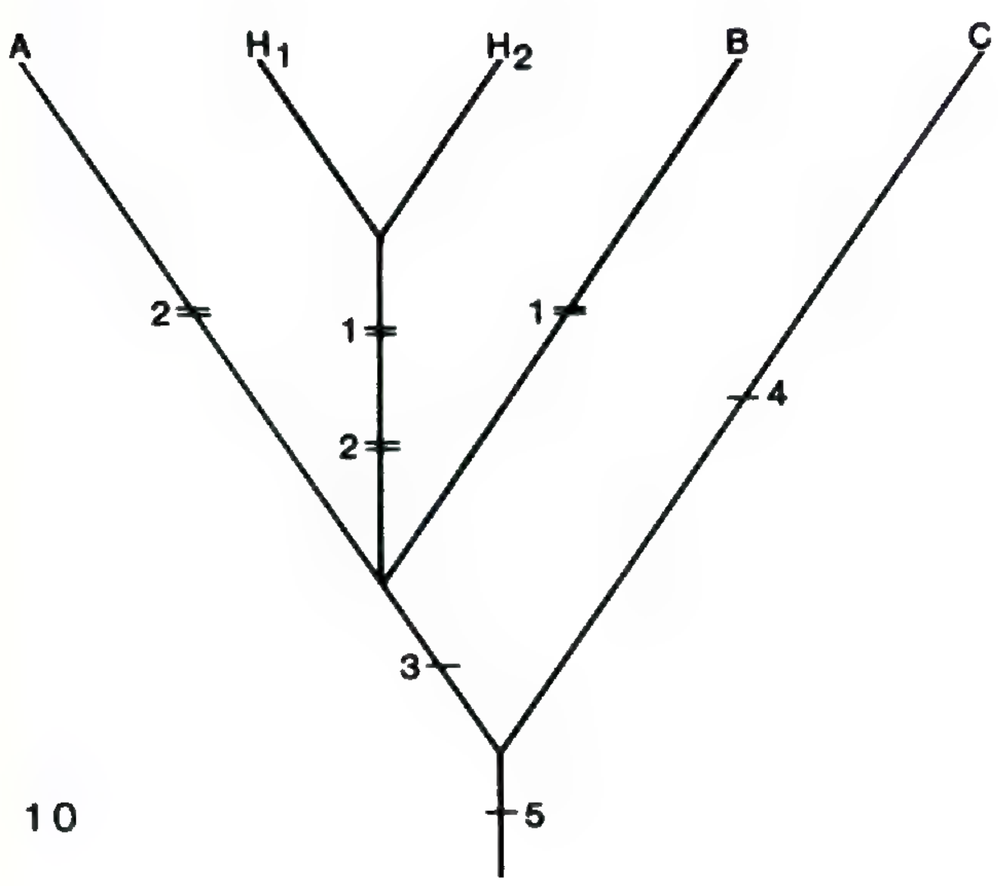

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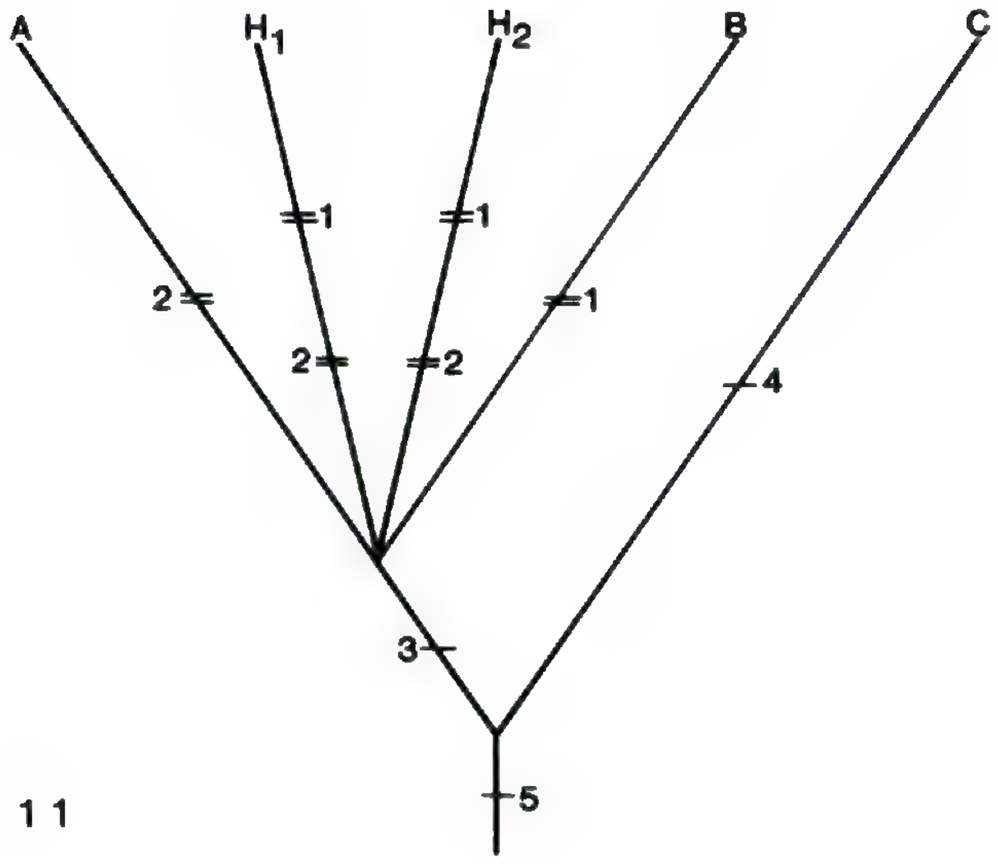

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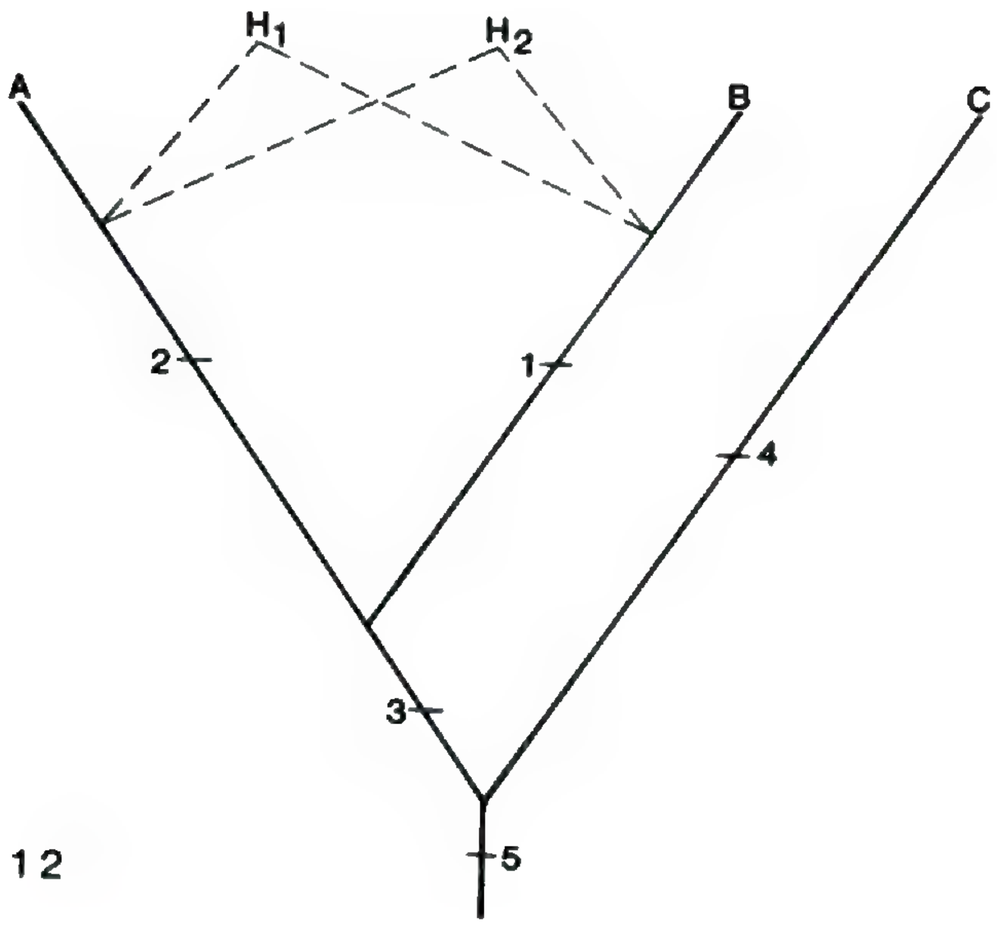

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FIGURES 8–12. Cladograms illustrating some of the results when the same two parent species (A and B) produce more than one hybrid, H1 and H2.

mosome number, karyotyping, and pollen fertility before they can be referred to as hybrids.

Nelson (1983) has suggested a method for analyzing cladograms for possible hybrids. His procedure begins with the most parsimonious cladogram without a reticulation and continues by adding reticulations one at a time so as to minimize character conflict. It is based on the idea that when there are two equally parsimonious ways of representing a homology on a cladogram

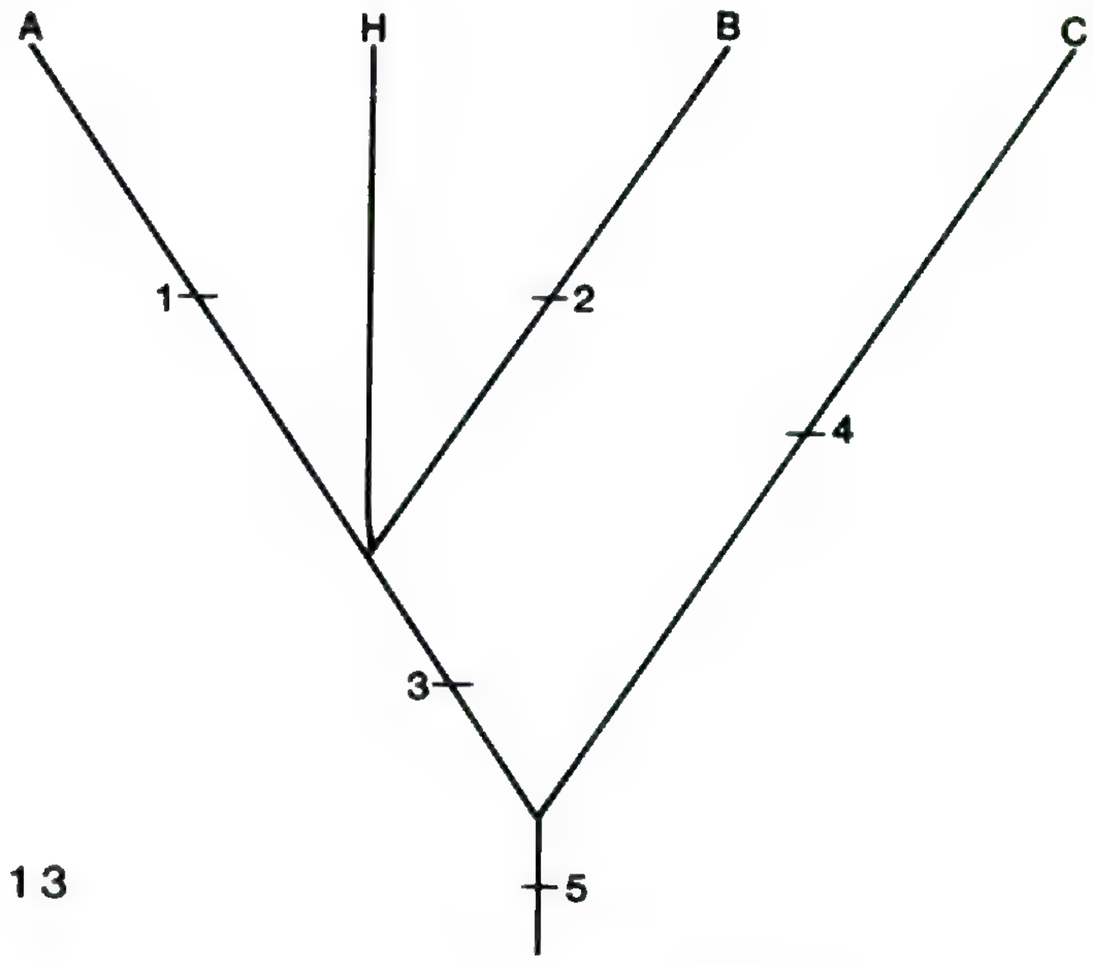


FIGURE 13. Cladogram illustrating that it is more parsimonious to have a polytomy when the hybrid does not show any of the autapomorphies of either parent.

one should investigate the possibility of inserting a reticulation. If the reticulation results in a decrease of apparent homoplasy and if the taxon exhibits character conflict of the "intermediate" type, the reticulation can be maintained. For a certain set of data (Appendix H) there are two equally parsimonious cladograms, with the same branching pattern. One cladogram (Fig. 20) has a parallel acquisition of character 4 (Figs. 20–22, Appendix H) and the other has one acquisition of character 4 and a subsequent loss (Fig. 21). However, one can introduce one reticulation and eliminate the need for homoplasy and/or loss (Fig. 22). All this diagram indicates is that *if* hybridization is involved it is most likely that taxon B is of hybrid origin.

A more complicated example involves nine taxa and 12 characters. There are two equally parsimonious cladograms with the same branching pattern with different amounts of homoplasy and loss (Figs. 23, 24; for characters for Figs. 23–25 see Appendix I). By progressively adding reticulations, all need of reversal and/or homoplasy can be eliminated. Taxa H and I may be hybrids (Fig. 25). Nelson's method of examination of character conflict is only a beginning.

Microloma illustrates the use of the Nelson method to change the cladogram in Figure 26 (for characters for Figs. 26, 27 see Appendix J) to the one in Figure 27 by adding one reticulation and thereby shortening the cladogram.

Some groups have characteristics that cause difficulties when using Nelson's method. For instance, some have their origin in hybridization but have since speciated (developed autapomorphies), some have numerous hybrids and even hybridization among hybrids, and some hybrids do not have all of the apomorphies of the parents (as in Fig. 2). The workability of Nelson's method is dependent on the hybrid inheriting the apomorphic characters from the parent taxa without too many character losses; otherwise the cladogram with the reticulations (Fig. 28; for characters for Figs. 28, 29 see Appendix K) will be longer than the most parsimonious cladogram without reticulations (Fig. 29). Also, this method is only feasible when the percentage of hybrids in the data set is low because the possibilities become endless, especially when the hybrids are hybridizing.

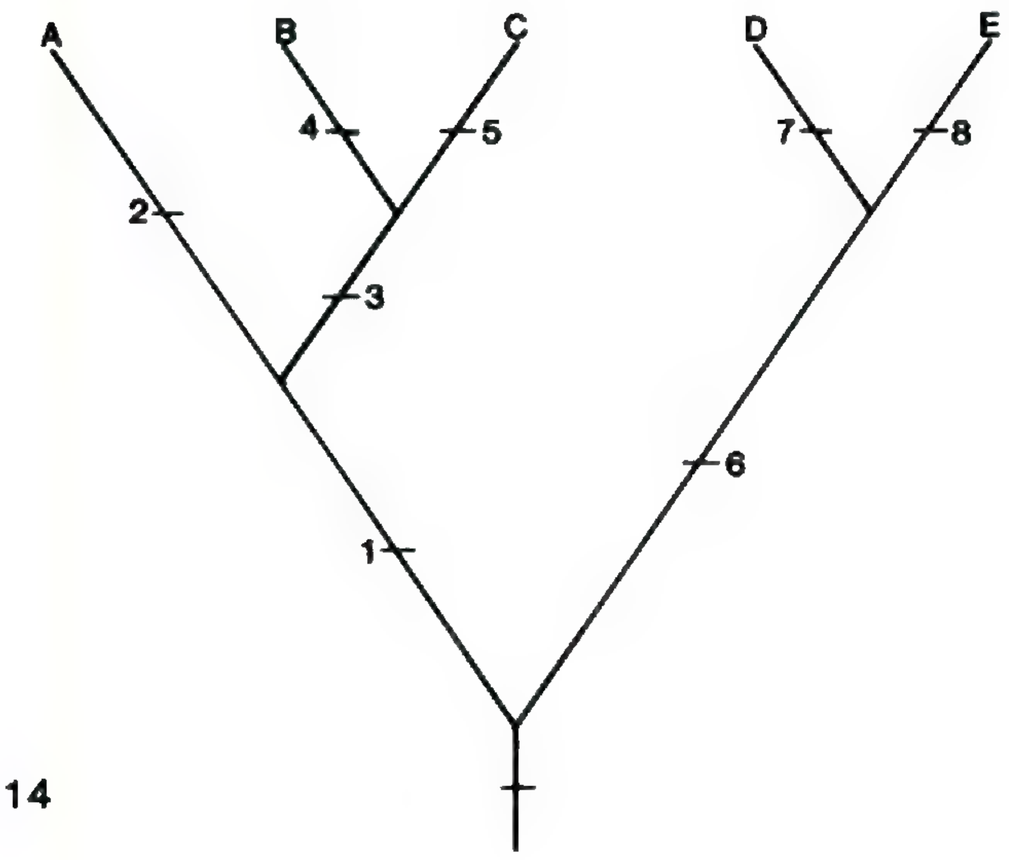
There are additional guidelines and methods that can be used when examining cladograms for possible hybrids. Use of these on seven data sets indicates that insights into the identification of possible hybrids and their parents can be gained by studying the character patterns of the cladograms as well as the distributions and ploidy levels of the taxa involved. Some of these guidelines and methods are elaborations and evaluations of previously published ideas and others are new.

GUIDELINES AND METHODS FOR IDENTIFYING POSSIBLE HYBRIDS AND THEIR PARENTS

1. When there are two cladograms of similar length and one taxon position changes, the taxon that is moving may be a hybrid and the two taxa between which it is moving may be the parents. In Figures 3 and 4, taxon H (the hybrid) shifts between taxa A and B in the two most parsimonious cladograms. Taxon H may be a hybrid and A and B may be its parents. In Figures 15 and 16 taxon H shifts between taxa C and D and may be a hybrid.

2. As an extension of number 1, it is possible to follow a path of character conflicts. Figure 15 has characters 6 and 7 appearing twice and this identifies taxon D, the parent with which H (the hybrid) is not grouped. Figure 16 has 1, 3, and 5 appearing twice and this identifies taxon C, the parent with which H is not grouped. You do not have to have all of the characters. For instance, in Figure 16, H might not have character 3 (Fig. 30; for characters for Figs. 30, 31 see Appendix L) but as long as it had 1 and 5 taxon C would emerge as the other parent (Fig. 31).

3. Taxa that are defined solely by character conflicts may be hybrids or parents. In Figure



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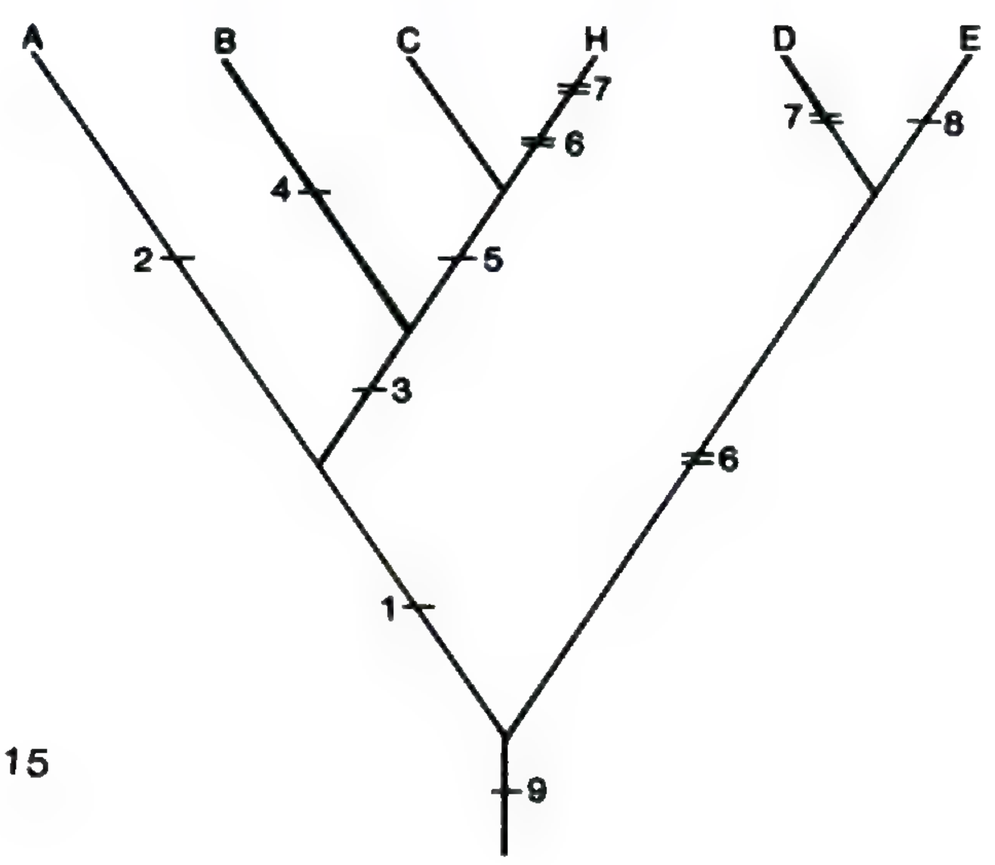

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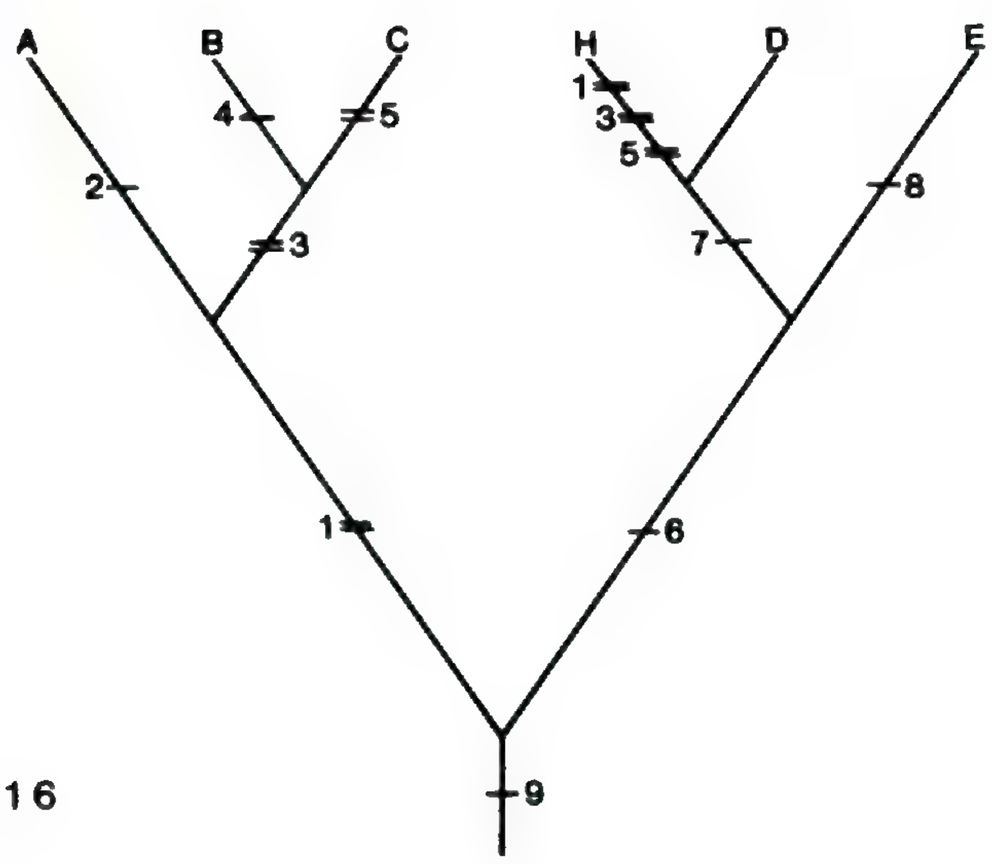

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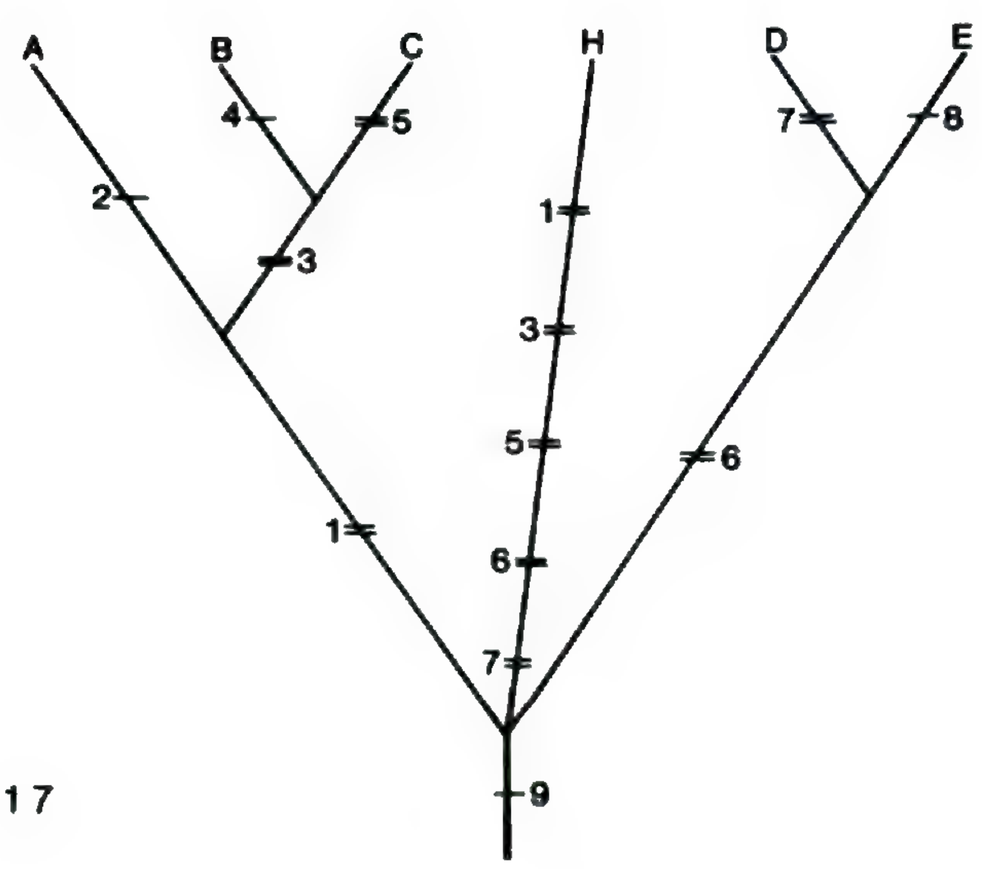

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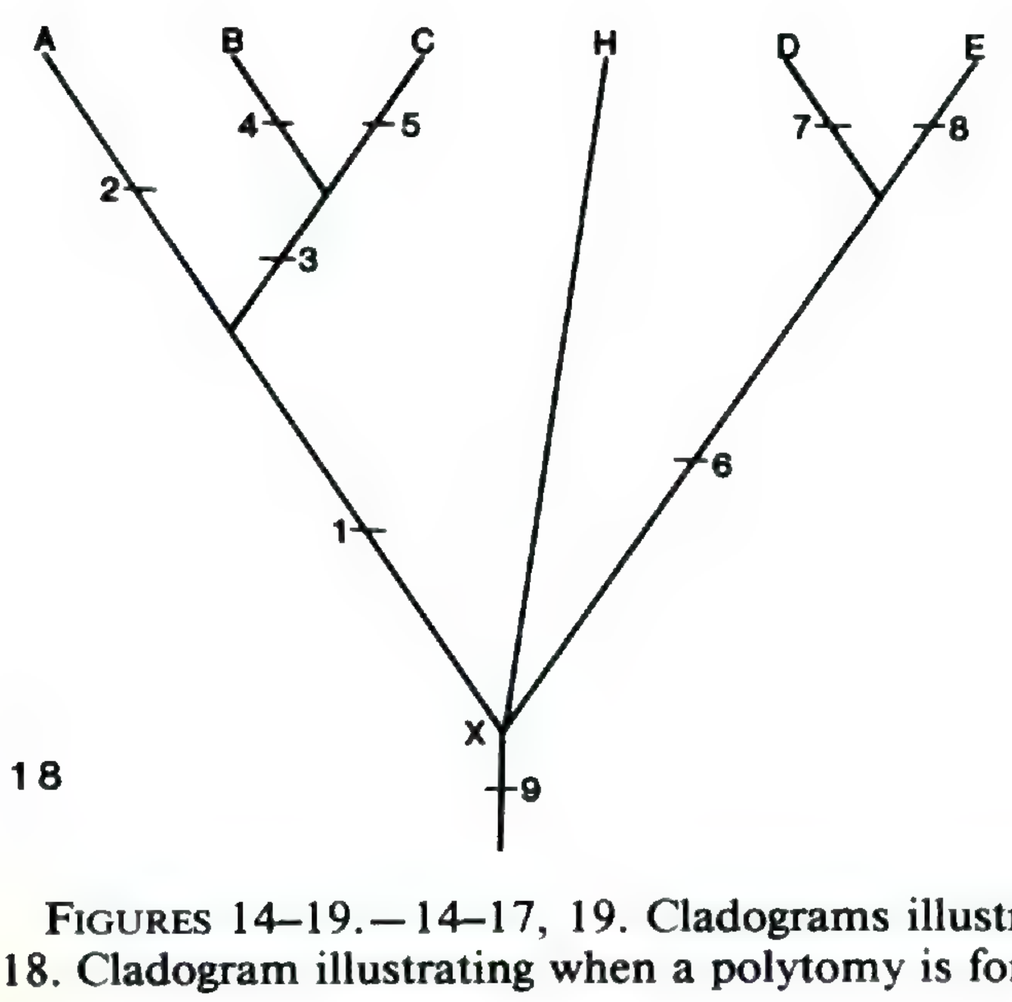

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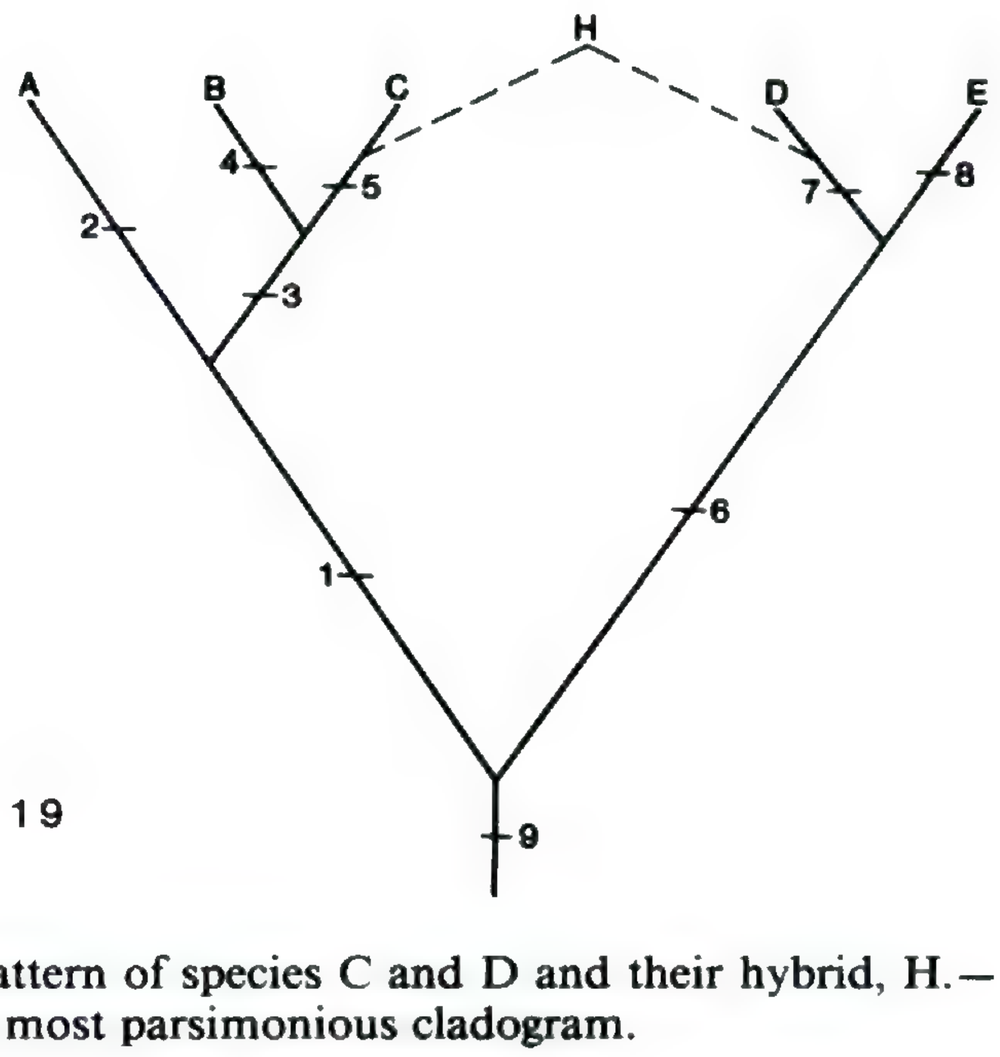

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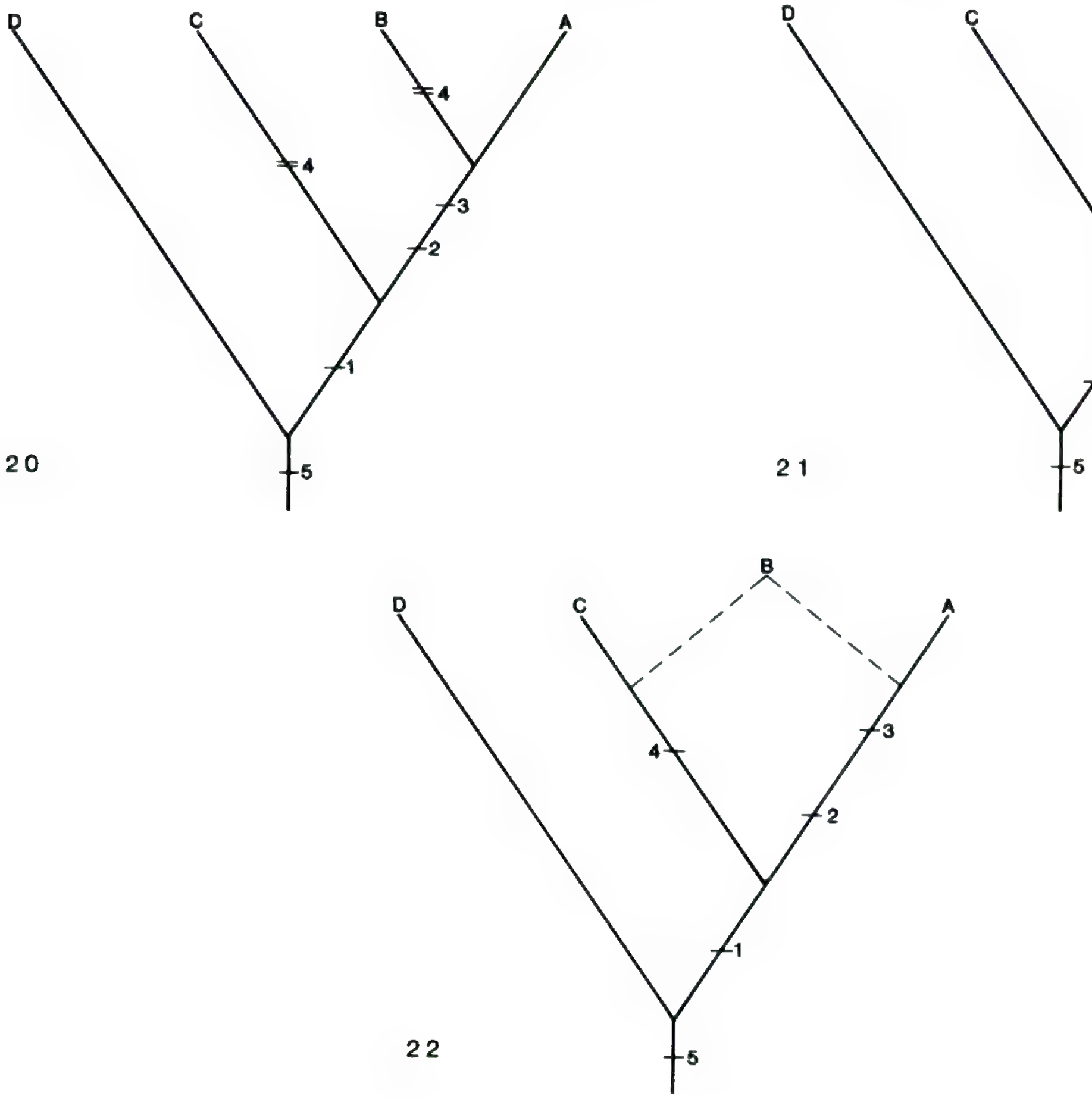
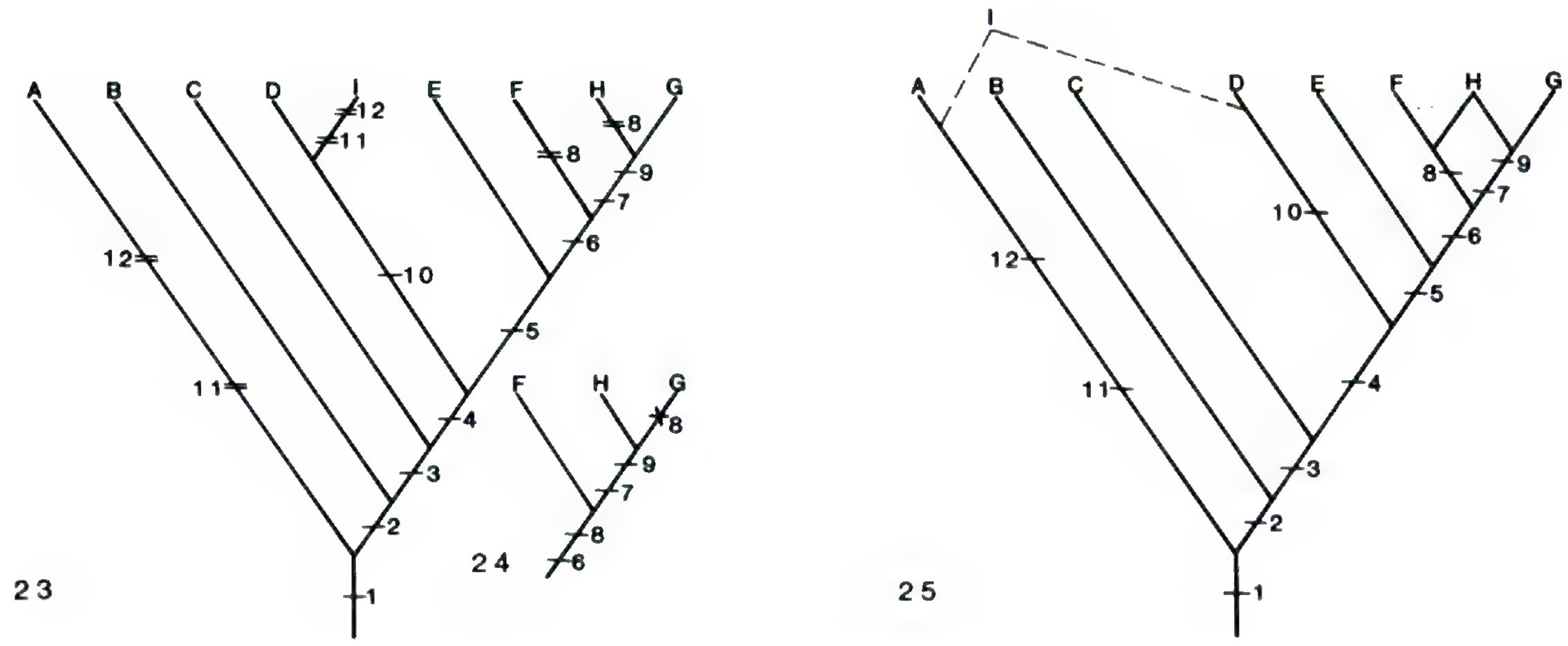
FIGURES 14–19.—14–17, 19. Cladograms illustrating the pattern of species C and D and their hybrid, H.—18. Cladogram illustrating when a polytomy is formed in the most parsimonious cladogram.

15, taxa H (the hybrid) and D are defined only by characters that appear elsewhere on the cladogram and in Figure 16, taxa C and H also have only homoplasies. The same is true for taxa C and B in Figure 20, taxa A and I in Figure 23, and taxa B and C in Figure 26.

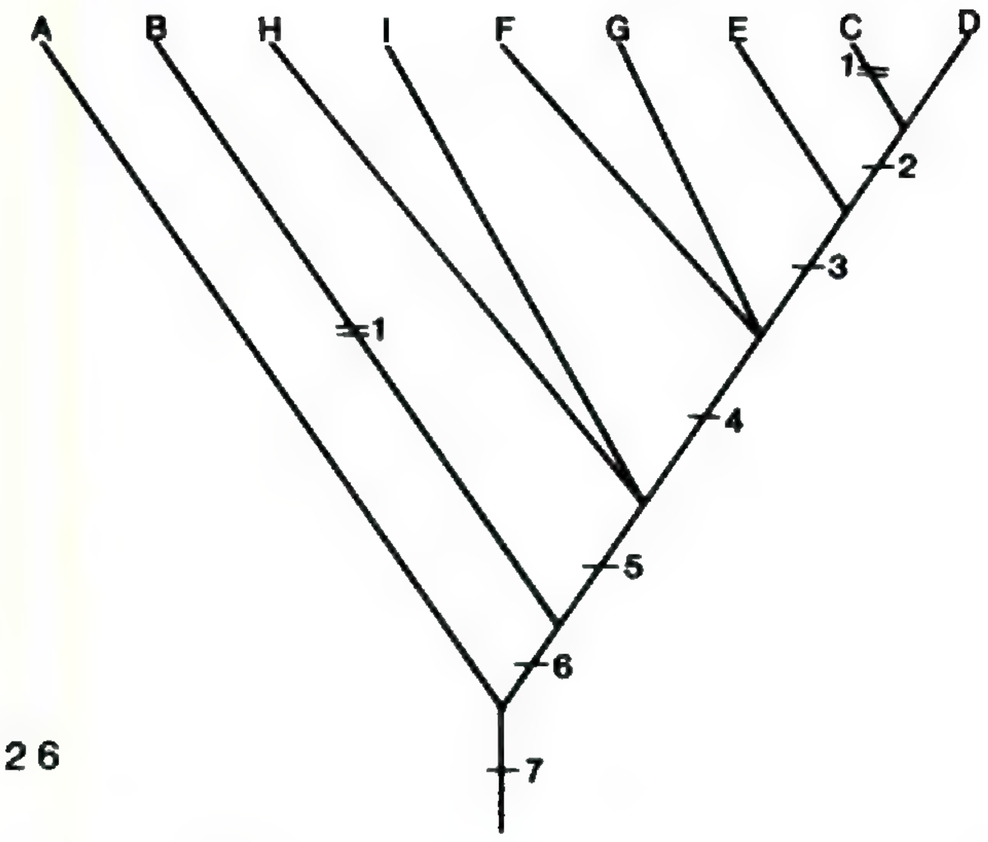
4. Taxa with reversals may be hybrids. In Figure 32 (for characters for Figs. 32, 33 see Appendix M) taxon H (the hybrid) has not inherited all of the apomorphies of both parents and therefore is defined not only by characters that appear more than once on the cladogram but also by



FIGURES 20–22. Cladograms illustrating a simple example of the Nelson (1983) method for analyzing cladograms for possible hybrids.



FIGURES 23–25. Cladograms illustrating an example of the Nelson (1983) method for analyzing cladograms for possible hybrids.



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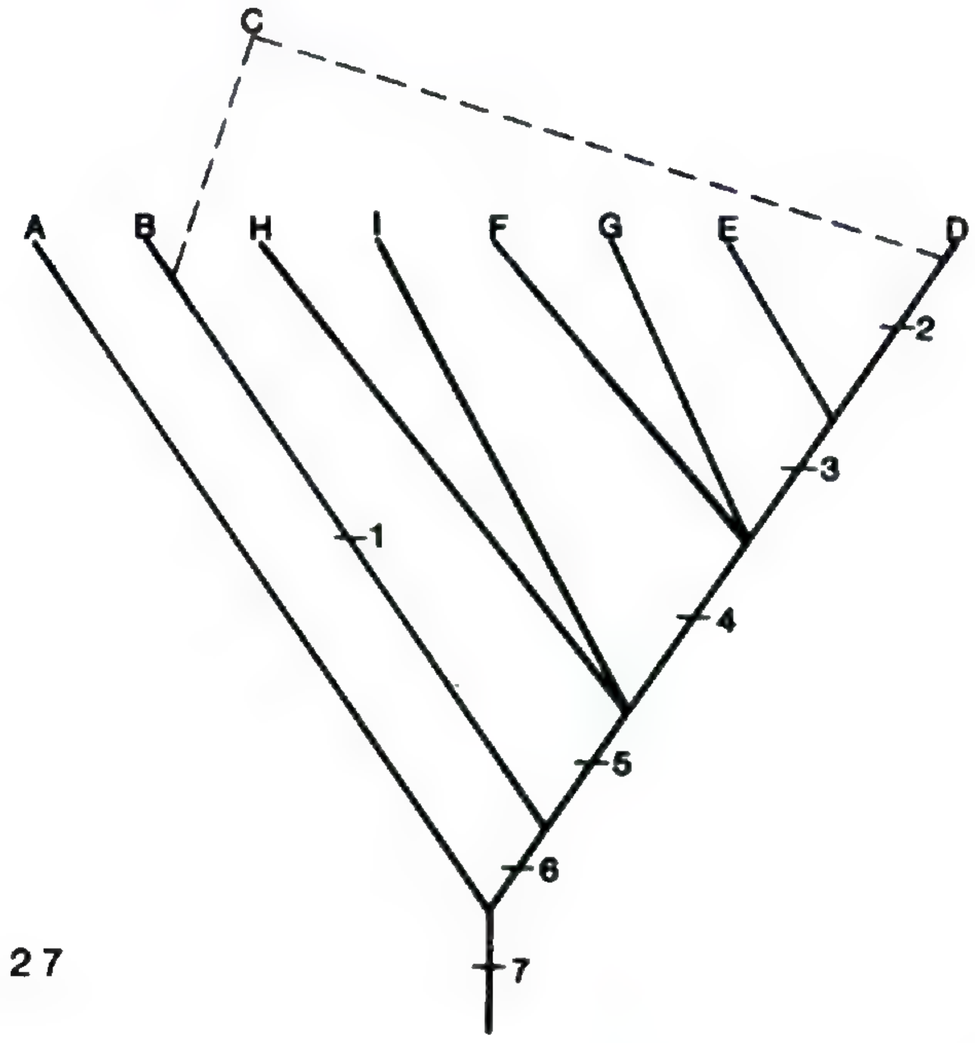

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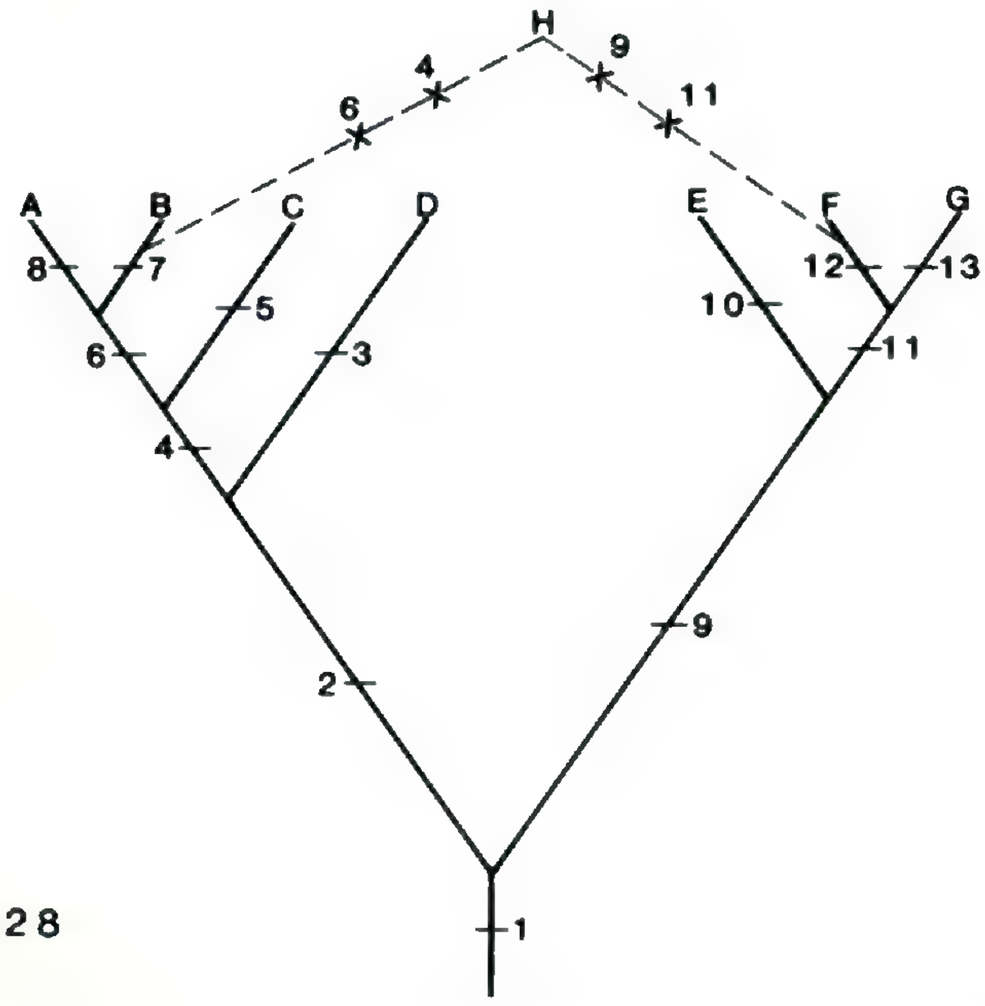
FIGURES 26, 27. Cladograms illustrating the use of Nelson's method for analyzing cladograms for possible hybrids in the genus *Microloma*.

character loss. Taxon H does not have characters 3 and 8 from taxon C and is also missing character 10 from taxon D. In fact, there has been enough inheritance of plesiomorphies to make the cladogram with reticulations (Fig. 33) the same length as the most parsimonious cladogram (Fig. 32). Another possibility is when there is one parent species rich in apomorphies and another lacking them altogether—hybrids might be intermediate or they might evidence multiple loss.

5. Taxa without autapomorphies may be parents. If the hybrid inherits all of the apomorphies of the parent with which it is grouped, then the parent will have no autapomorphies (Fig. 2, taxon A; Fig. 7, taxon A; Fig. 15, taxon C; Fig. 16, taxon D). If the hybrid fails to inherit any of the apomorphies of the parent with which it is not grouped, the hybrid will have no autapomorphies (Fig. 13, taxon H)—normally in evidence as homoplasies.

6. Consensus Trees—Consensus analysis is developing rapidly as an aid in evaluating a number of equally or nearly equally parsimonious cladograms. Consensus trees represent the information shared by two or more cladograms. The consensus tree is a compromise classifica-



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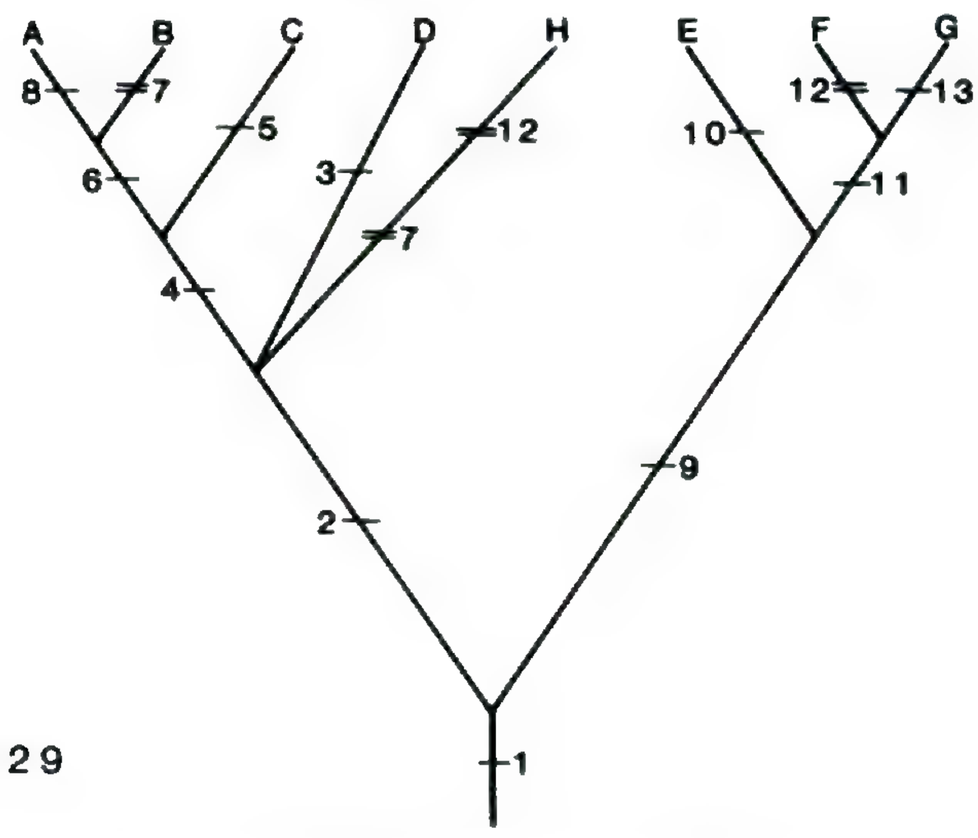

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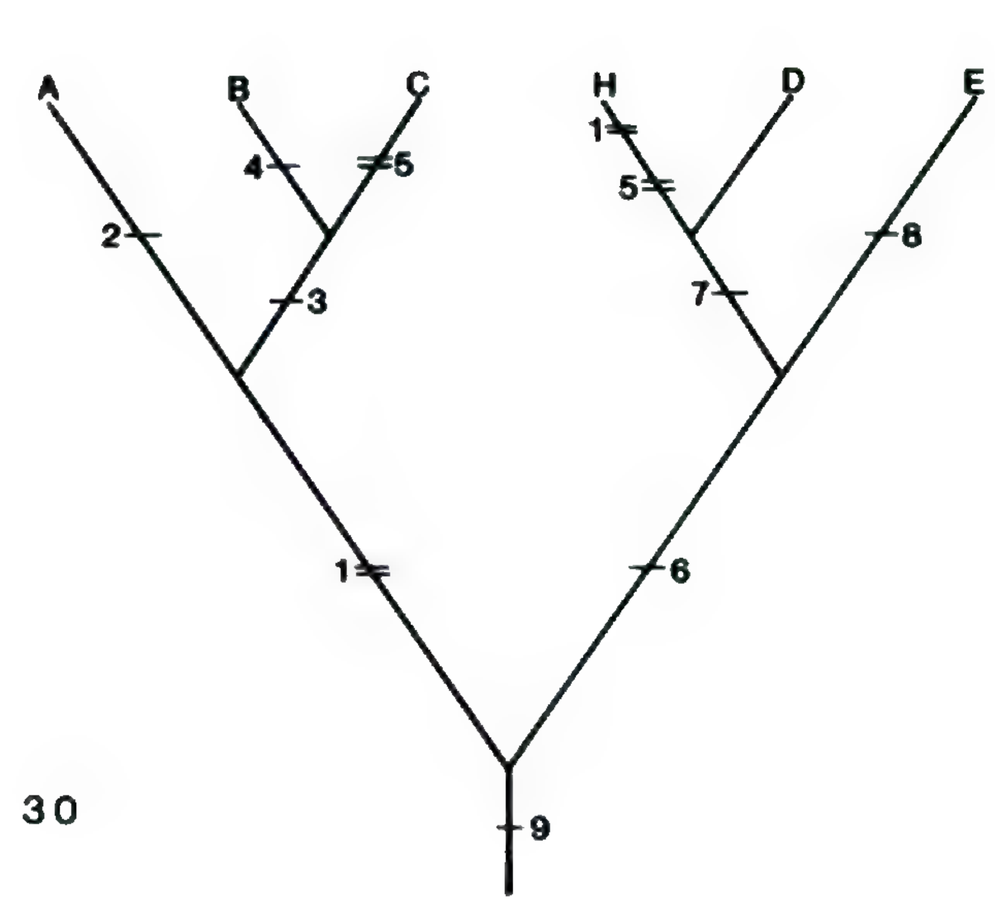
FIGURES 28, 29. Cladograms illustrating that the cladograms with reticulations are not necessarily the most parsimonious.



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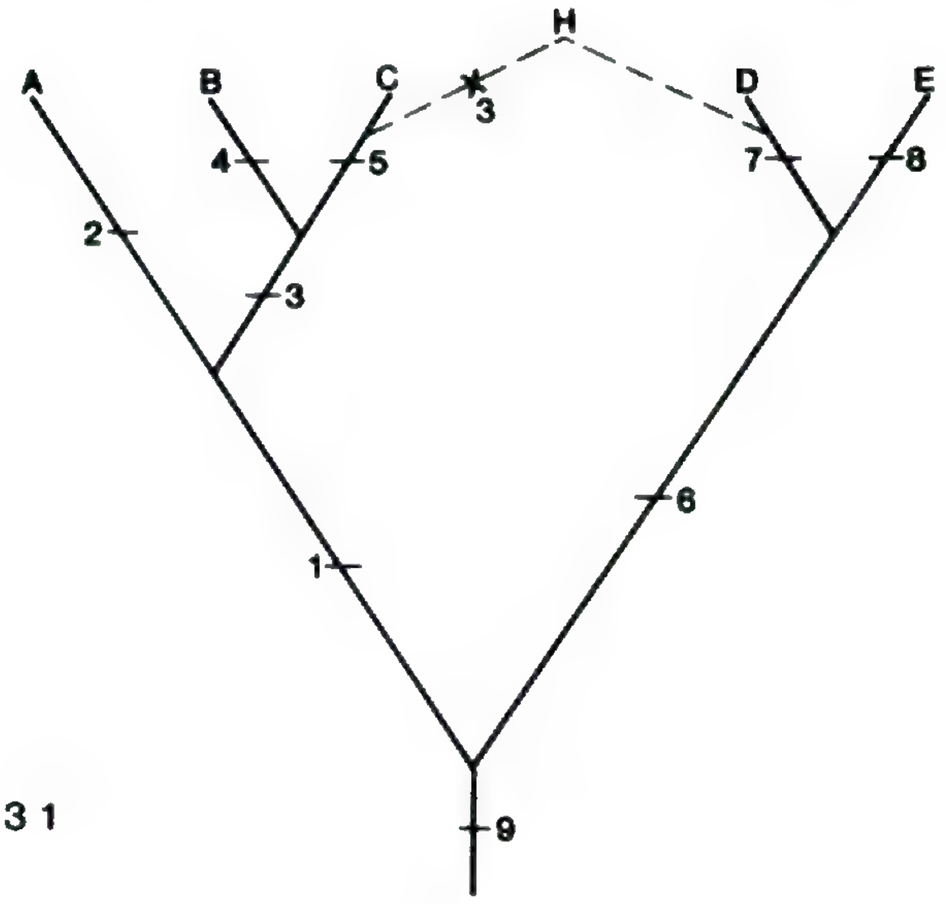

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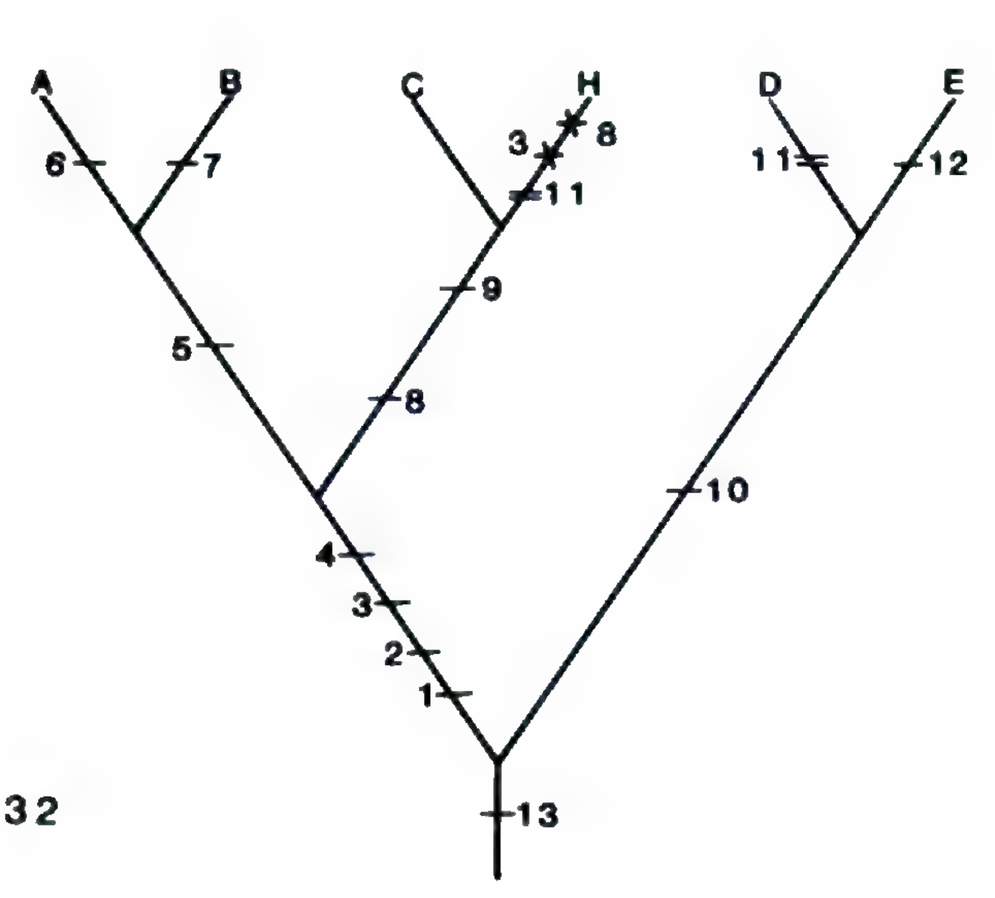
FIGURES 30, 31. Cladograms illustrating that possible parents can be identified even if all apomorphies of both parents are not present in the hybrid.

tion. Consensus trees were first developed by Adams (1972) and have been used in the context of comparing cladistic versus phenetic methods (Mickevich, 1978; Schuh & Polhemus, 1980; Sokal & Rohlf, 1981) or to compare a cladogram constructed from a chemical data set and an intuitive tree (Seaman & Funk, 1983). There are many different types of consensus analysis, Adams consensus (Adams, 1972), strict consensus (Sokal & Rohlf, 1981), majority consensus (Margush & McMorris, 1981), and *durchschnitt* consensus (Neuman, 1983). Only Adams consensus trees and Nelson component analysis will be discussed in this paper because of ease of use and explanation. For further investigation, other references include Mickevich (1978), McMorris et al. (1983), and a series of papers in Felsenstein (1983).

An Adams consensus tree (ACT) may have a topology different from any of the cladograms used to construct them. Figures 15 and 16 have a different topology, but if we concentrate on agreements we get Figure 14. Then we can add the taxon left out to the first node common to both of its positions (Fig. 17). A detailed discussion of how to construct an ACT is found in Adams (1972).

7. Component Analysis (NCA) was developed by Nelson (1979) as a consensus method. A component is any monophyletic group on a cladogram or phylogenetic tree. Every cladogram can be divided into a certain number of components that have more than one terminal taxon. In order to construct a Nelson Consensus Tree it is possible to add together components that are common to two or more cladograms. The



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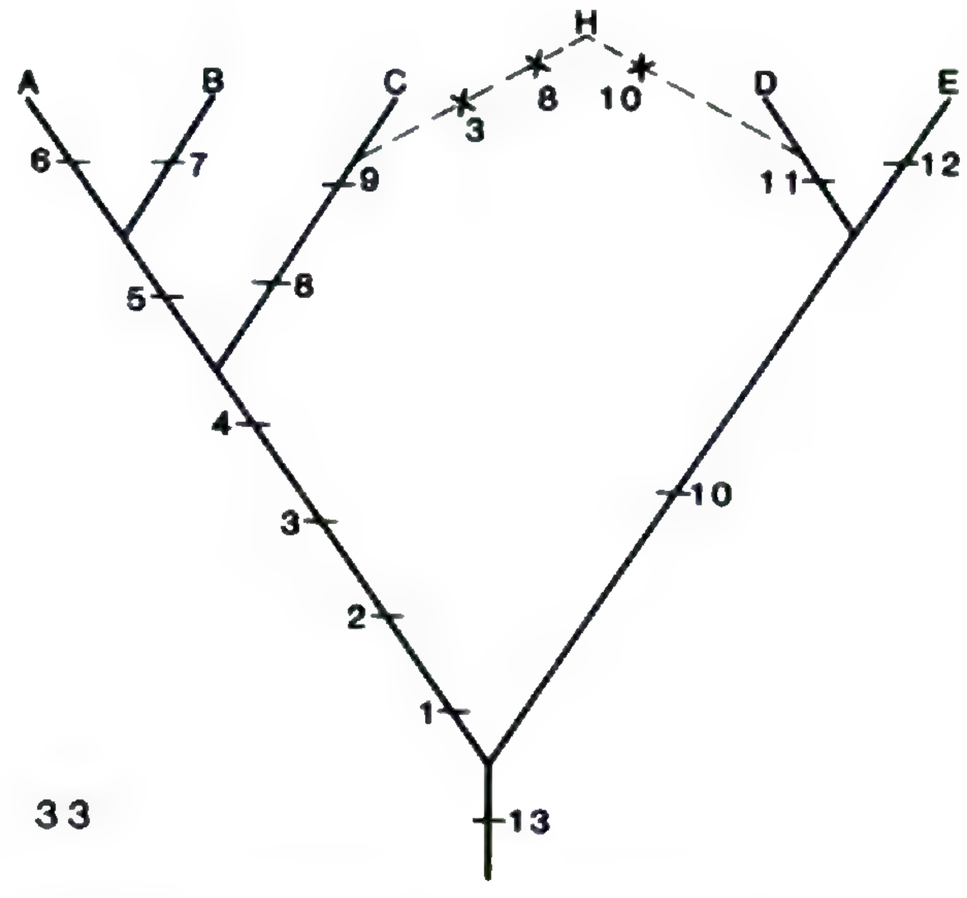

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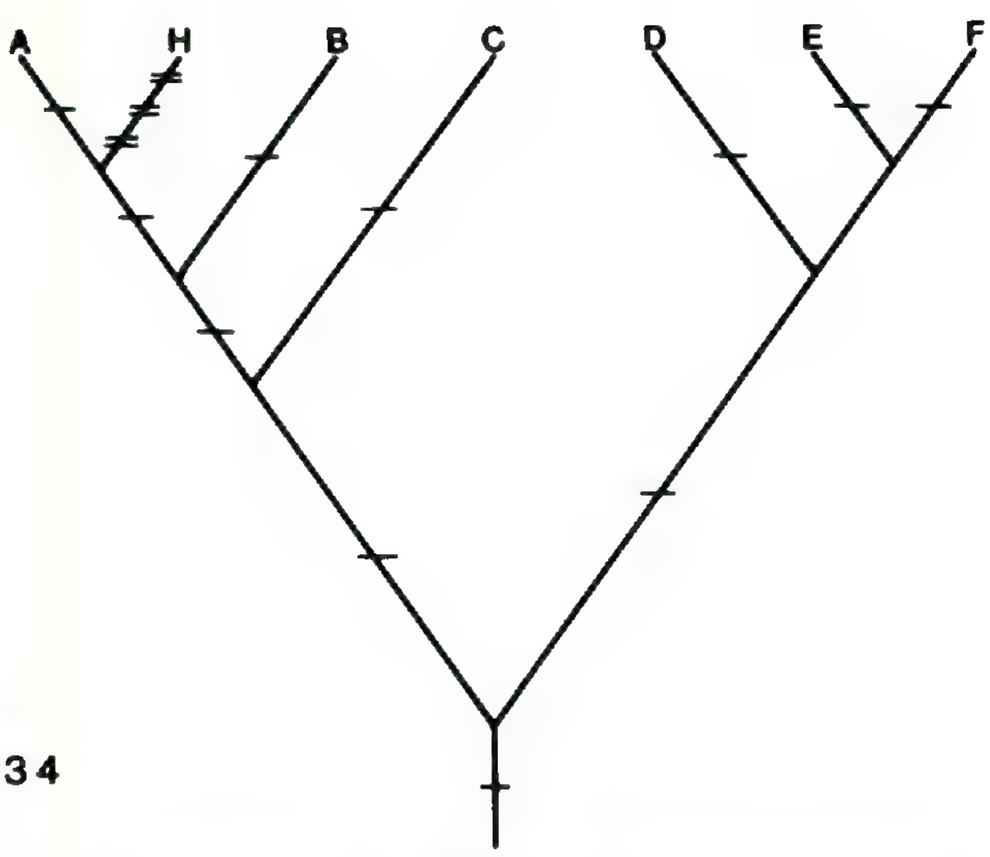
FIGURES 32, 33. Cladograms illustrating that character loss may be an indication of hybridization.



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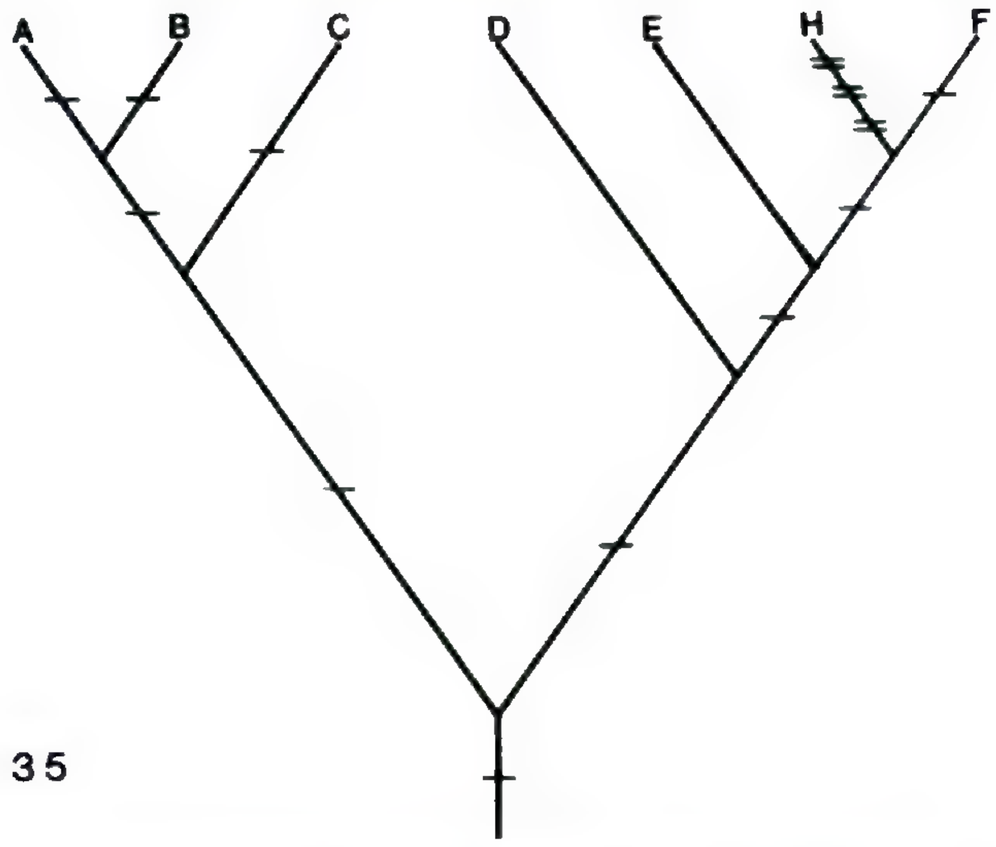

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FIGURES 34, 35. Cladograms illustrating that by comparing the components (Table 1) one can identify the source of incompatibility.

movement of one taxon from one side of the cladogram to the other can have the effect of changing all of the components (Figs. 34, 35, Table 1) and no consensus tree can be constructed. However, instead of searching for complete agreement among the components, we can examine in what way they are different and identify which taxa are responsible for the lack of congruence. Examining the list of components for the two figures (Figs. 34, 35, Table 1) it is obvious that taxon H is causing the incompatibility.

These various suggestions are not to be used individually but collectively to generate hypotheses of hybridization. We can then turn to other forms of data to corroborate or falsify our hypotheses. Two of the most readily available in many groups are distribution and polyploidy, but others such as karyotyping and pollen fertility can be employed. We will see how such information can be used in the examples below. All cladograms were constructed manually.

EXAMPLE 1. *MICROLOMA* (ASCLEPIADACEAE) BREMMER AND WANNTORP (1979)

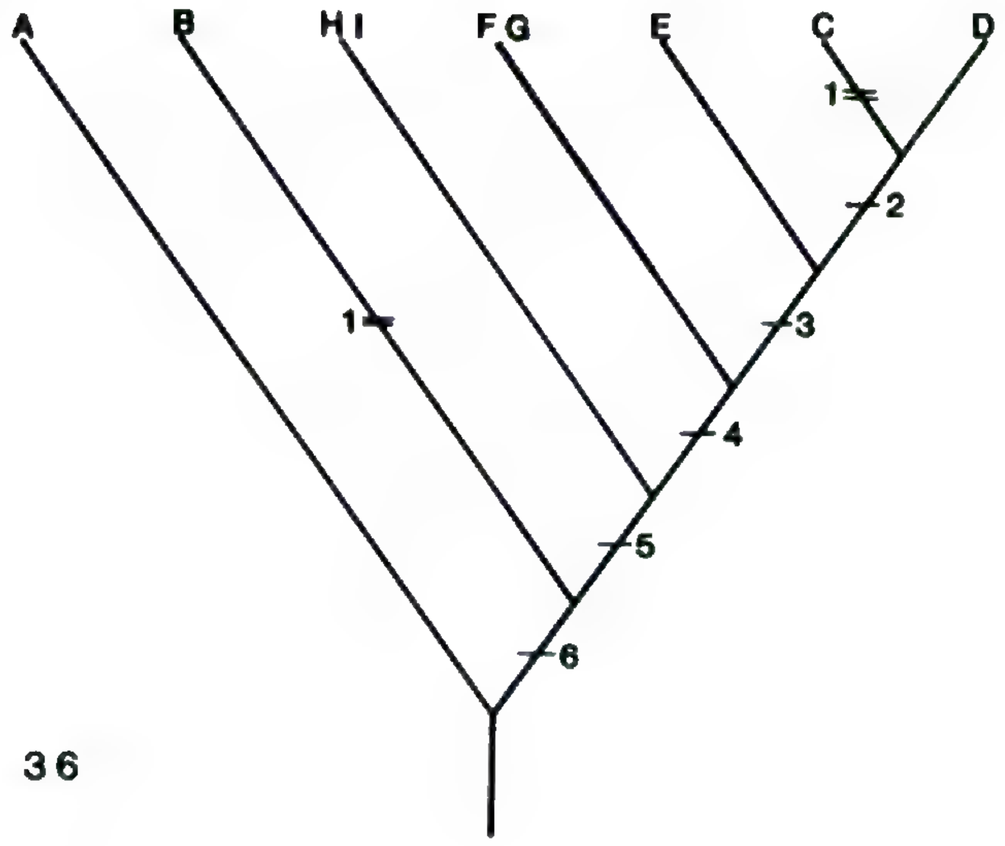
Microloma is an African genus of 19 species, nine of which are represented in the most parsimonious cladogram (Fig. 36, Appendix J) and an alternative cladogram that is three steps longer (Fig. 37). Figure 37 shows taxon C sharing an apomorphy with taxon B and Figure 36 shows taxon C sharing four apomorphies with taxon D indicating that B and D may be the parents if C is a hybrid. Also, there is a path of parallel characters to follow to the parents especially in Figure 37. Furthermore, taxon D (Fig. 36) and taxon B (Fig. 37) have no autapomorphies, indicating they might be the parents with which the hybrid is grouped. In addition, an ACT (Fig. 38) can be constructed that identifies the hybrid by placing it at the first node shared by the two parents. A NCA (Table 2) shows that C is responsible for the incompatibility between the two sets of components.

EXAMPLE 2. *ANACYCLUS* (ASTERACEAE) HUMPHRIES (1979, 1981)

Anacyclus (Appendix N) is a genus of Mediterranean distribution with 14 species (Figs. 39–42). The monograph and subsequent paper by Humphries (1979, 1981) included a cladistic analysis and speculations on the hybrid origin for three of the species. Figure 39 is the most parsimonious cladogram (L = 45) for the data furnished by Humphries (1983); the number in parentheses next to the lower case letter indicates the number of apomorphies that have that pattern of distribution. If we concentrate on the character types that conflict with the most parsimonious cladogram (p, b, f, q, l) we can draw alternative cladograms that are slightly longer (Fig. 40, L = 50; Fig. 41, L = 52). Figure 40 has four character types in conflict (k, p, q, o) and a

TABLE 1. Components for Figures 34, 35.

Figure 34	Figure 35
AH	AB
AHB	ABC
AHBC	HF
EF	EHF
DEF	DEHF



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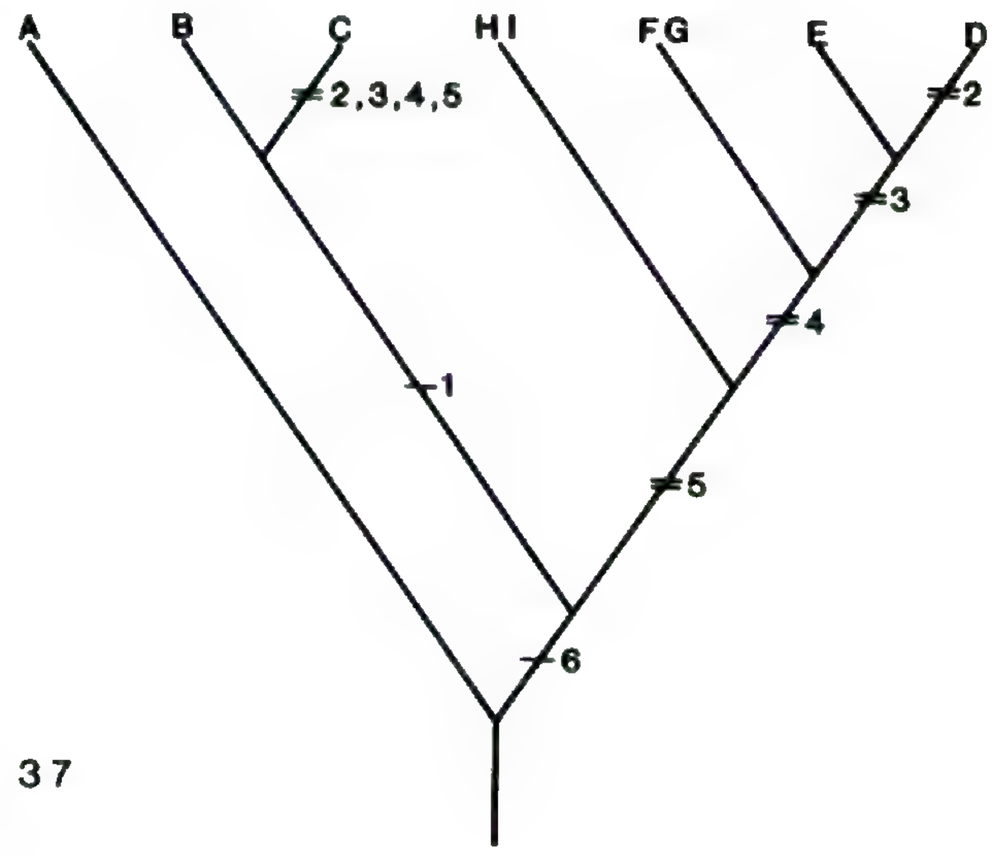

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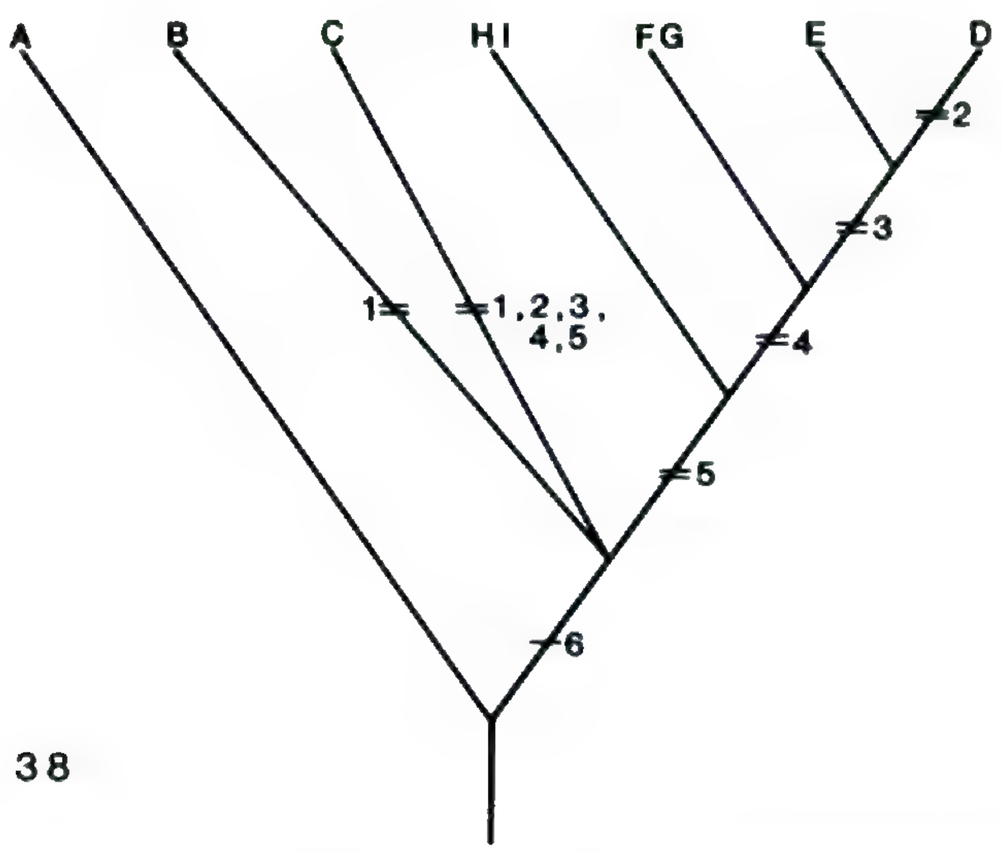

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FIGURES 36–38. Two cladograms of *Microloma* and their Adams consensus tree.

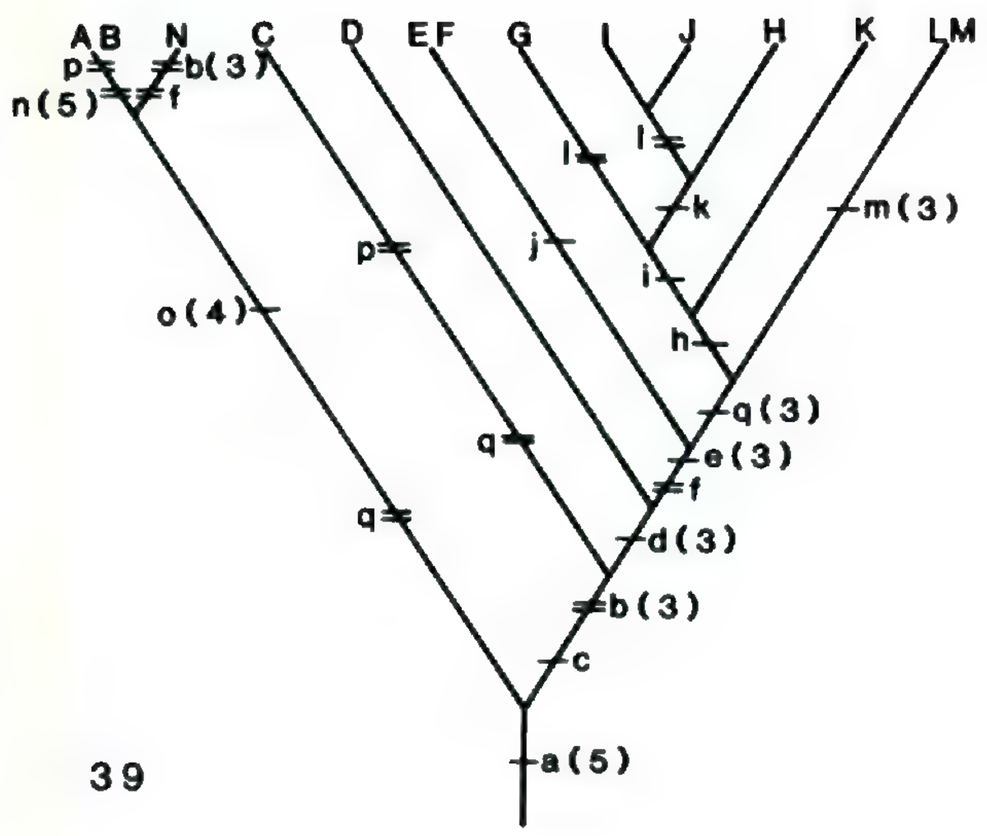
gain and subsequent loss of two character types (c, d). Figure 41 also has four types of conflict (o, b, c, q) and two types of loss (c, d). The consensus tree for these three cladograms is illustrated in Figure 42 and shows that four taxa are potential hybrids (N, C, I, J) because they have dropped in resolution and because they are defined either completely or primarily by characters that are found elsewhere on the cladogram. In addition by listing the components of the three figures (Table 3) it is evident that all of the component incompatibility is caused by taxa I, J, C, and N. These four taxa are potential hybrids (Fig. 43) and their possible parents are as follows:

possible hybrids		possible parents
N	=	AB × EF-LM
I	=	G × H
J	=	G × H
C	=	AB × D-LM

Figure 43 is 42 steps long. Based on his analyses Humphries (1979, 1981) suggested three putative hybrids (N, I, J) and indicated corroboration for the hypothesis of hybridization for these three species. According to Humphries in addition to sharing apomorphies with AB and EF-LM, *A. officinarum* (N) is known only as an extinct cultivar grown in the nineteenth century for pharmaceutical reasons. *Anacyclus valentinus* (I) and *A. inconstans* (J) have florets of intermediate length between *A. clavatus* (G) and *A. homogamos* (H). Also, *A. valentinus* (I) is a weedy taxon

TABLE 2. Components for Figures 36, 37.

Figure 36	Figure 37
CD	BC
ECD	ED
FGECD	FGED
HIFGECD	HIFGED
BHIFGECD	BCHIFGED
ABHIFGECD	ABCHIFGED



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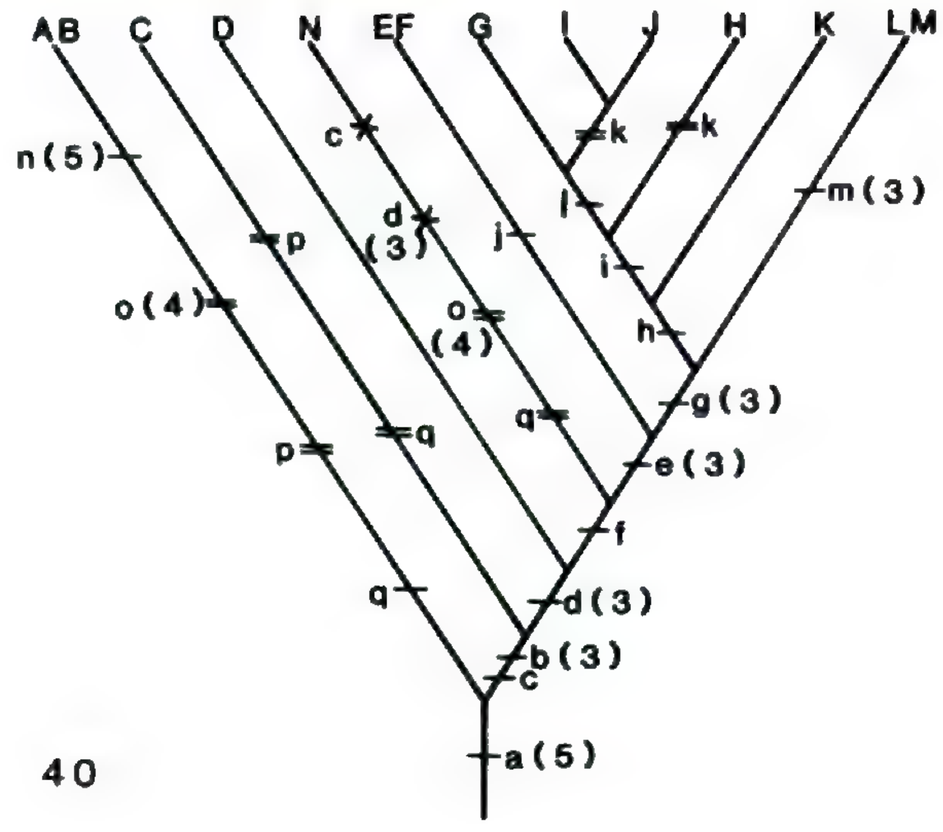

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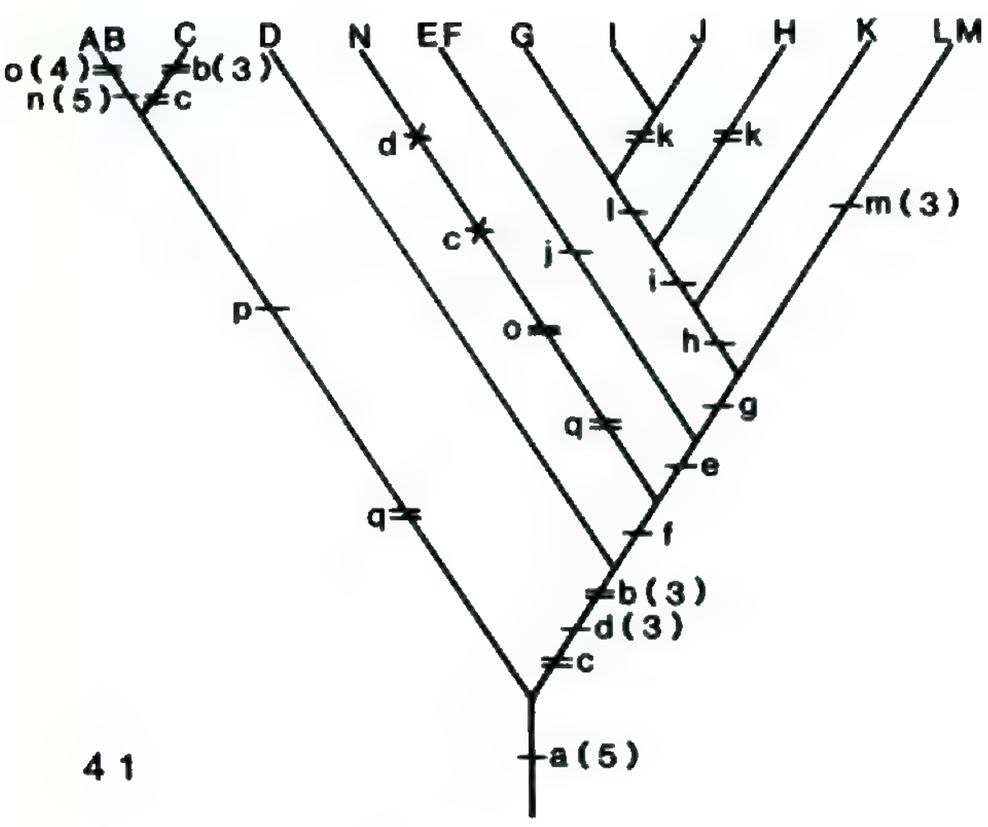

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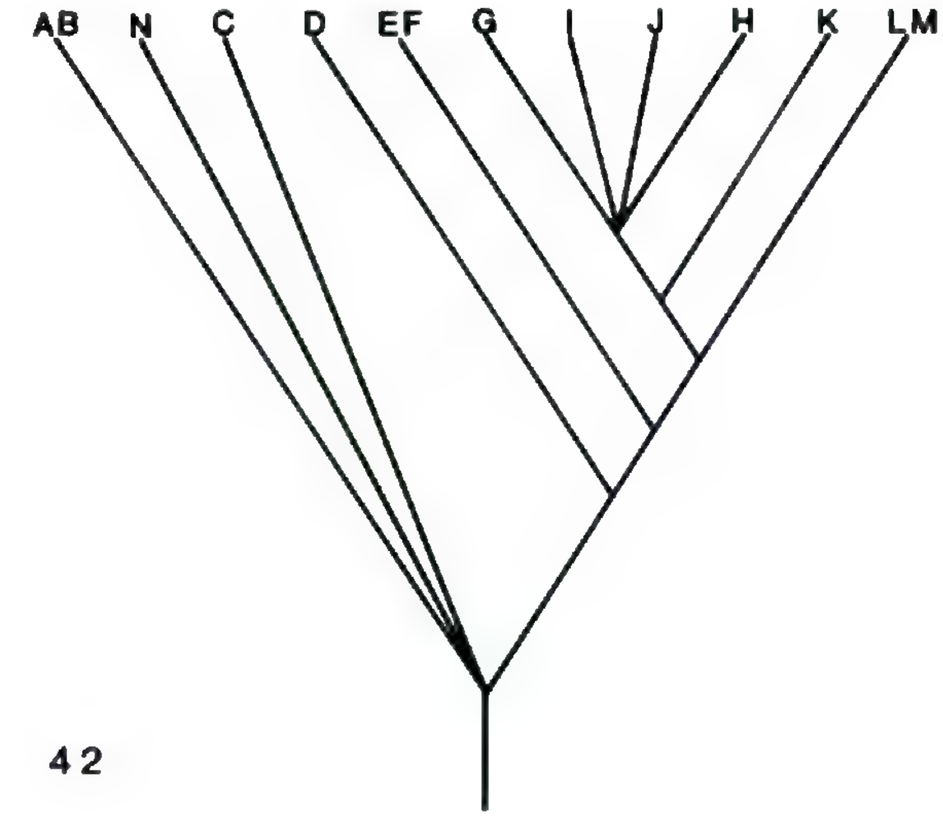

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FIGURES 39–42. Cladograms of *Anacyclus*.

occurring only on disturbed land in the southwest Mediterranean region, and *A. inconstans* (J) occurs sympatrically with the Algerian population of *A. clavatus* (G). Cytogenetic studies carried out by Humphries (1981) corroborated the hypotheses of hybridity for *A. valentinus* (I) and *A. inconstans* (J). There was no material for cytogenetic studies available for either *A. officinarum* (N) or *A. monanthos* (C). There is, then, good reason to list both *A. valentinus* (I) and *A. inconstans* (J) as possible hybrids because the hypotheses of hybridity have been supported by independent data. *Anacyclus officinarum* (N) has been supported as a hybrid by its cultivated nature but is more difficult to analyze because it is not known to be extant. *Anacyclus monanthos* (C) was not indicated by Humphries to be of hybrid origin. In his monograph, Humphries

TABLE 3. Components for Figures 39–41.

Figure 39	Figure 40	Figure 41	Conflicts
IJ	IJ	IJ	
IJH	GIJ	GIJ	IJ
GIJH	GIJH	GIJH	IJ
GIJHK	GIJHK	GIJHK	
GIJHKLM	GIJHKLM	GIJHKLM	
EFGIJHKLM	EFGIJHKLM	EFGIJHKLM	
DEFGIJHKLM	NEFGIJHKLM	NEFGIJHKLM	N
CDEFGIJHKLM	DNEFGIJHKLM	DNEFGIJHKLM	C, N
ABN	CDNEFGIJHKLM	ABC	C, N
ABNCDEFGIJHKLM	ABCDNEFGIJHKLM	ABCDNEFGIJHKLM	

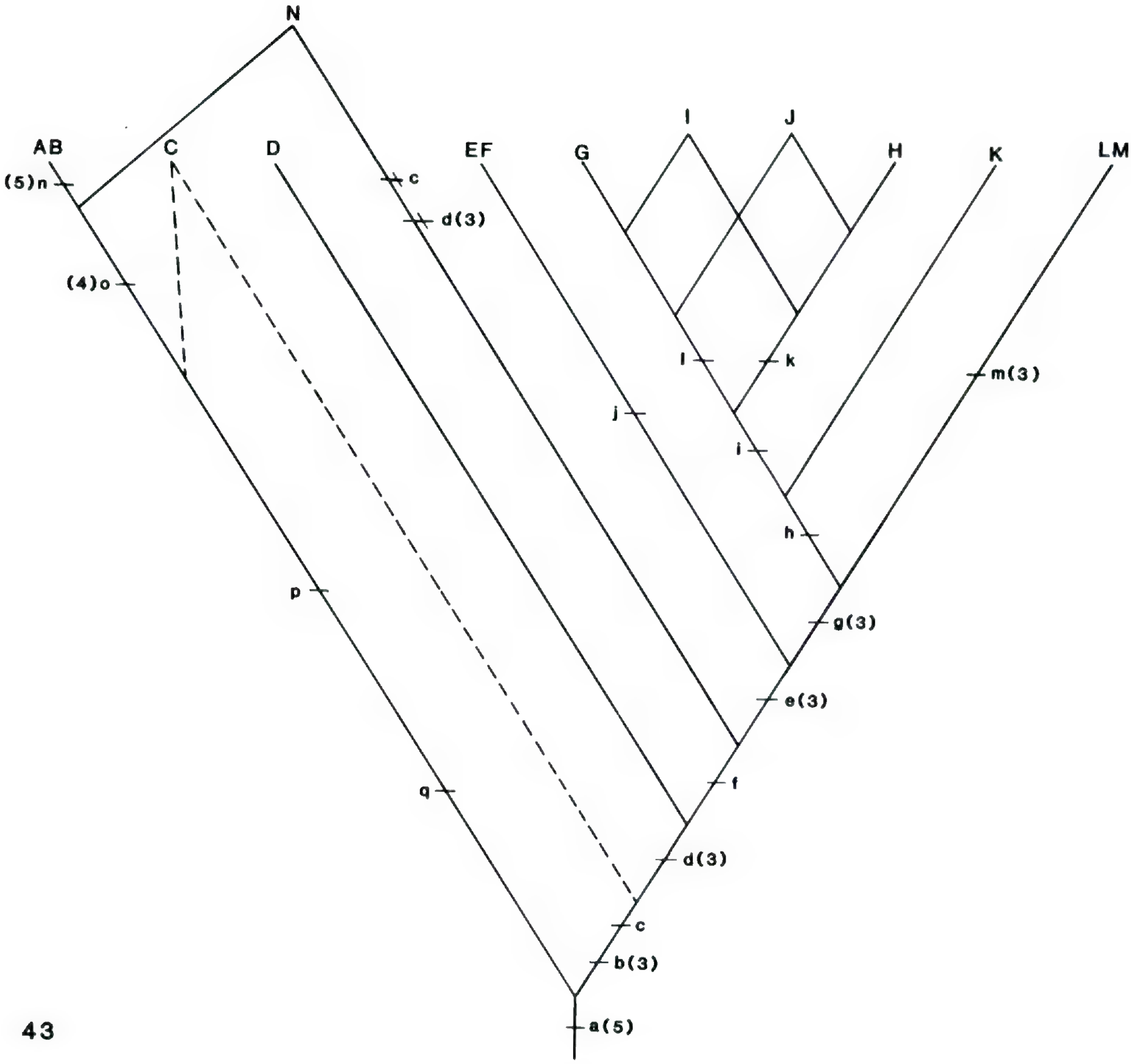


FIGURE 43. Cladogram of *Anacyclus* with reticulations.

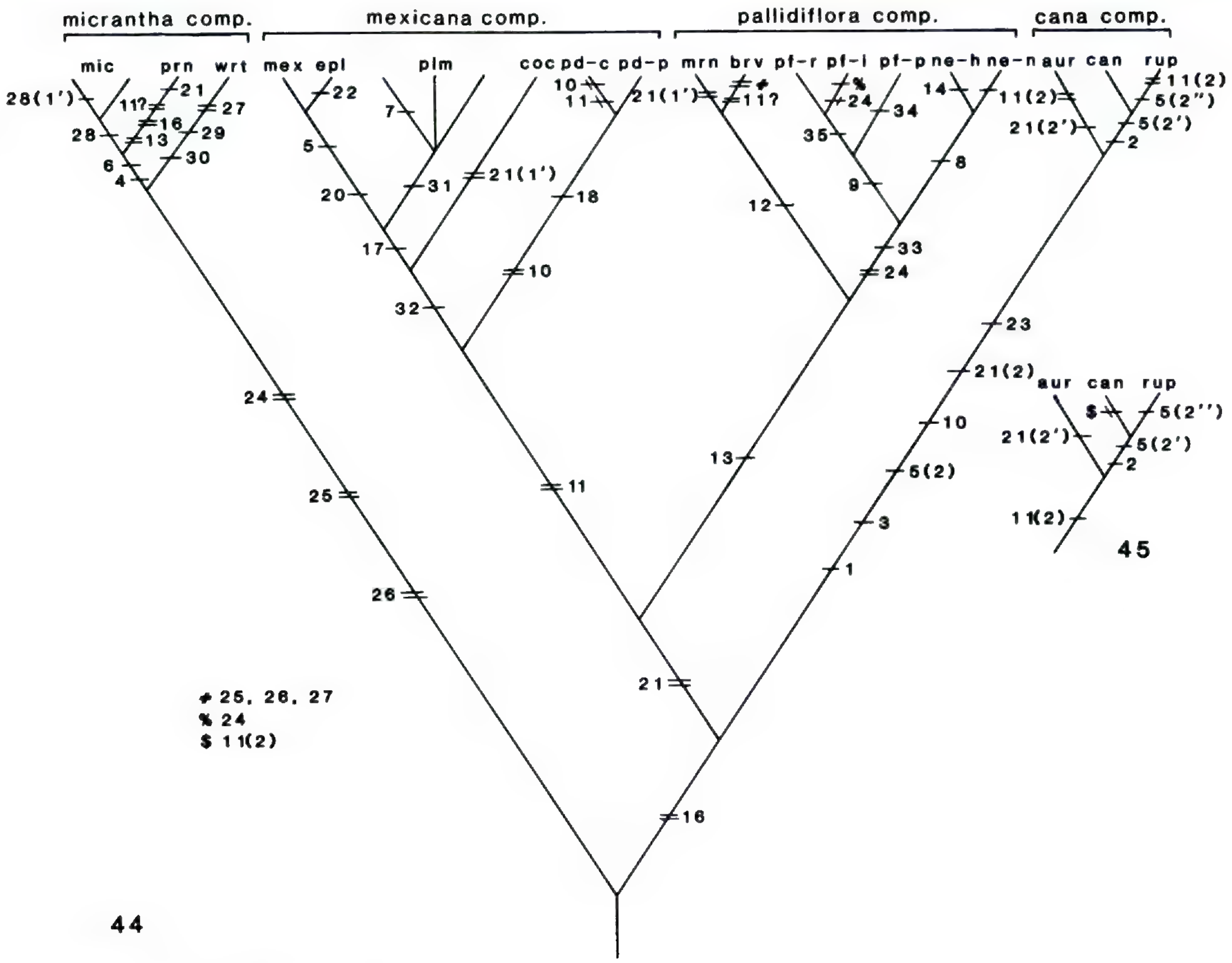
(1979) listed it as a pioneer of sandy soil and in some areas a dominant weed; these are characteristics of some hybrids. He also mentioned that it resembles one of the two subspecies of *A. homogamos* (H). However, Humphries thinks that *A. monanthos* (C) is a taxon exhibiting intermediate characters and not a hybrid because it has many autapomorphies (Humphries, pers. comm.). Because of the lack of additional information on this taxon I have left it as a dotted line on the cladogram (Fig. 43).

The cladogram in Figure 43 differs from that of Humphries because I emphasized reducing the number of parallel characters and was not as concerned if this created additional character losses. Therefore, taxon N is connected as an internode further along the diagram. This is important because it is, in my opinion, unlikely that a hybrid will inherit all of the apomorphies of both parents. Thus, some plesiomorphies will be inherited resulting in the loss of some characters. The apomorphies that are inherited are the guide to the identification of possible parents.

Anacyclus is a good example of the use of cladistics to identify possible hybrids and then employing other techniques including karyotyping and chemical analysis, distribution, and habitats to further corroborate or falsify the hypotheses of hybridization (Humphries, 1979, 1981).

EXAMPLE 3. *AGASTACHE* (LAMIACEAE) SANDERS (1982, AND IN PREP.)

The 14 species of *Agastache* Clayt. sect. *Brittonastrum* (Appendix O) are all diploid and are confined to the cordilleras of the southwest United



FIGURES 44, 45. Cladograms of *Agastache*.

States and Northwest Mexico. Looking at the parsimony cladogram (Figs. 44, 45) there are taxa with no autapomorphies (*A. pallidiflora* var. *neomexicana* ne-n, *A. pallidiflora* var. *greenei* pf-r, *A. mexicana* mex), taxa with only character conflicts (*A. breviflora* brv, *A. mearnsii* mrn, *A. coccinea* coc, *A. pringlei* prn), and taxa with character losses (*A. pallida* var. *coriacea* pd-c, *A. pallidiflora* var. *gilensis* pf-i). Three of these taxa (prn, brv, pd-c) are immediately identifiable as possible hybrids, *A. pringlei* and *A. breviflora* because they have four character conflicts each and *A. pallida* var. *coriacea* because it has two character losses. Less strongly indicated are *A. pallidiflora* var. *gilensis* (because of the absence of character 24 and some connection with *A. coccinea*) and *A. mearnsii* [because of character 21(1')]. Examining each one individually, *A. breviflora* has characters 25, 26, and 27 (and sometimes 11). If *A. breviflora* is a hybrid then one parent (*A. mearnsii*) could be its sister species. In order to identify a candidate for the second parent, emphasize the characters *A. breviflora* has and not the characters it does not have. Then locate where else on the cladogram these characters are found (25, 26, and 27; Fig. 44). The presence of these three characters indicates *A. wrightii* (wrt) as the other possible parent. Comparing the geographical distributions (Sanders, pers. comm.), *A. breviflora* and *A. wrightii* are sympatric in southern Arizona, southwest New Mexico, and northern Sonora and Chihuahua. *Agastache mearnsii* is found a short distance from *A. wrightii* in southern Sonora and Chihuahua. The distribution pattern would suggest a hybridization event is possible.

A second possible hybrid, *A. pringlei* (prn) is sister to *A. micrantha* (one subspecies of which has no autapomorphies). *Agastache micrantha* has four character conflicts (13, 16, 21, and sometimes 11, see Appendix O). Locating the apomorphies on the cladogram identifies the "Pallidiflora complex," which contains *A. breviflora, A. mearnsii,* and the five subspecific taxa of *A. pallidiflora. Agastache pringlei* is sometimes sympatric with *A. micrantha* (southern

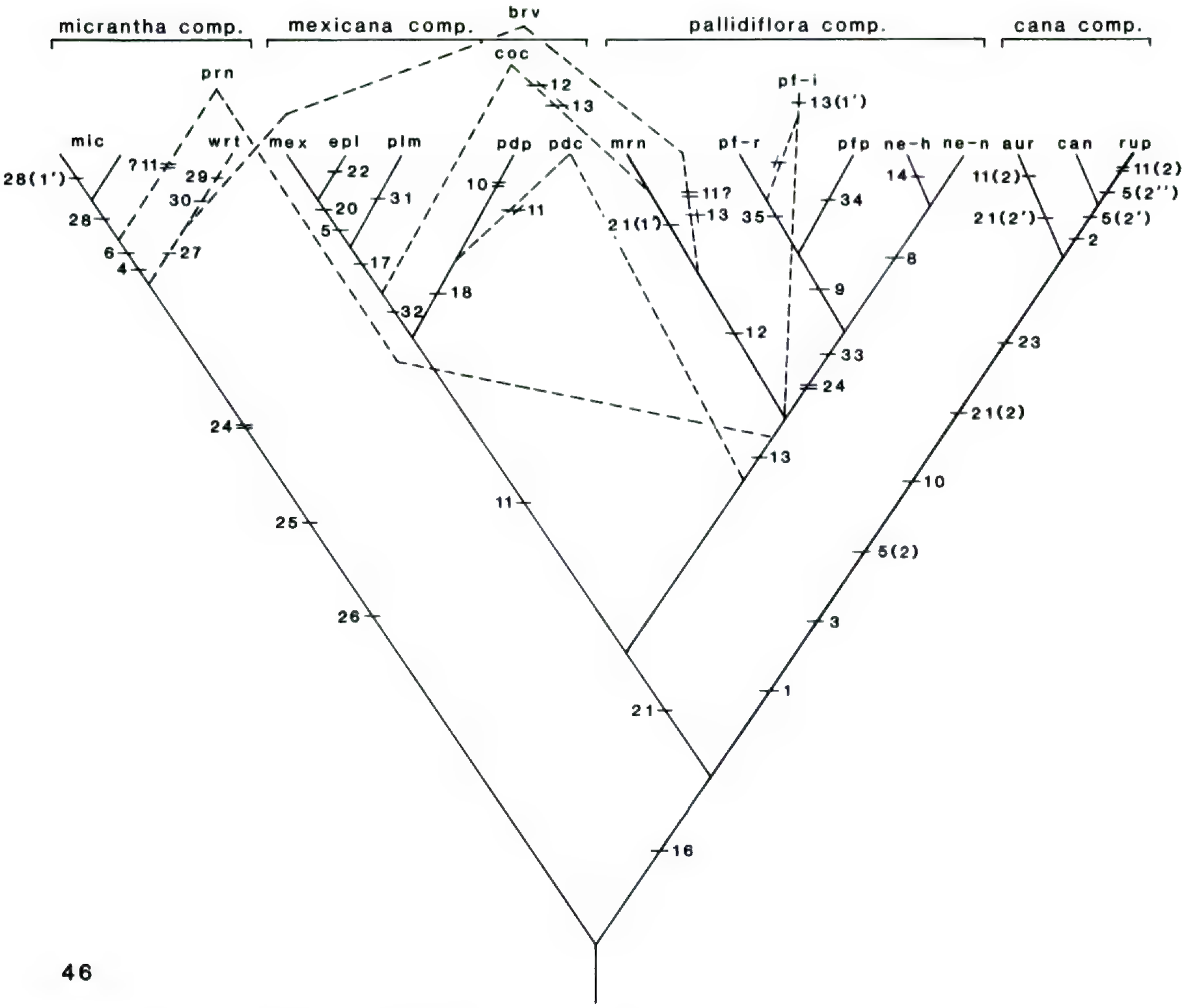


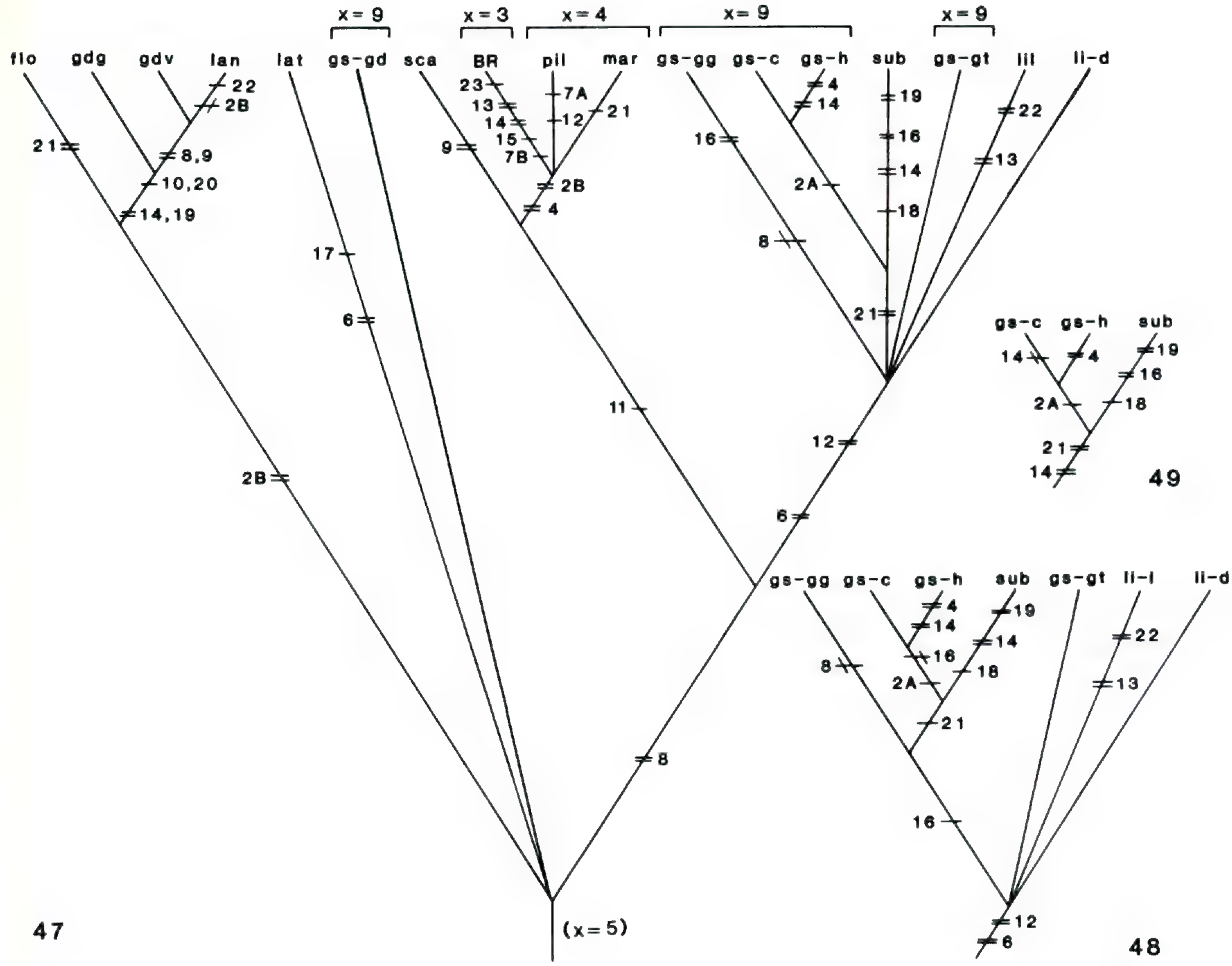
FIGURE 46. Cladogram of *Agastache* with reticulations.

Chihuahua and southern New Mexico) and parapatric with *A. mearnsii* (southern Chihuahua and the Chihuahua/Sonora border). The *A. pallidiflora* subspecific taxa and *A. breviflora* are distributed in the southwest United States. If *A. pringlei* is a hybrid the most likely putative parents are *A. micrantha* and *A. mearnsii.*

A third potential hybrid, *A. pallida* var. *coriacea* (pd-c), is sister to *A. pallida* var. *pallida* and has two character losses. If *A. pallida* var. *coriacea* is a hybrid and one parent is *A. pallida* var. *pallida* then the other parent is probably something that lacks characters 10 and 11; possibly something in the "Pallidiflora complex" because the putative hybrid has characters 16 and 21. Based on geographical distribution, the most likely parent in the "Pallidiflora complex" is *A. mearnsii* that has a parapatric distribution with *A. pallida* var. *coriacea.*

The last two possible hybrids, *A. coccinea* (coc) and *A. pallidiflora* var. *gilensis* (pf-i), are more difficult to place because they have less information (fewer characters). We can estimate that *A. coccinea* is a hybrid and that one parent may be found in the group defined by character 32; because of the presence of character 21(1') the other parent would probably be *A. mearnsii.* The distribution of the species does not help in this case because several of the taxa are sympatric.

The final taxon considered as a hybrid is *A. pallidiflora* var. *gilensis.* This taxon might be the result of a cross between *A. pallidiflora* var. *greenii* and some taxon without character 24. All taxa in the "Pallidiflora complex" that have a distribution that would allow for the formation of this hybrid have character 24 except *A. mearnsii.* However, *A. pallidiflora* var. *gilensis* has an autapomorphy, and this makes it less likely that it is of hybrid origin (but does not exclude it). Based on this analysis the following hybrids are pos-



FIGURES 47–49. Cladograms of *Chrysopsis* and *Bradburia*.

sible: brv = wrt × mrn, prn = mic × "Pallidiflora complex," pd-c = pd-d × mrn, coc = mrn × mex-plm, and pf-i = pf-r × some taxon without 24 (possibly mrn).

Figure 46 shows the hypothesized hybrids and their possible parents. According to Sanders (1981), the hybrids and their parents are as follows: brv = wrt × mrn, prn = mic × mrn, pd-c = pd-p × mrn, coc = pfr × mrn (mex-epl + mrn), and pf-i = pf-r × mrn (pf-f − pf-r + mrn). Although Sanders' estimates are in some cases more specific, there are no conflicts.

EXAMPLE 4. *CHRYSOPSIS* AND *BRADBURIA* (ASTERACEAE) SEMPLE (1981, AND PERS. COMM.), SEMPLE AND CHINNAPPA (1984)

Chrysopsis (Nutt.) Elliot (Appendix P; 10 species) and *Bradburia* Semple & Chinnappa (Appendix P; 1 species) are yellow-rayed golden-asters distributed in the southeast United States (especially Florida) except for one species of *Chrysopsis* that occurs in the eastern United States. Using the characters furnished by Semple three cladograms were constructed (Figs. 47–49). There is a high level of homoplasy in the cladogram because only nine apomorphies lacked character conflicts and only four of these 11 are synapomorphies (10, 20, 11, 2A). Such a high level of character conflict and character loss is an indication of possible hybridization. The chromosome numbers were not used as characters in the analysis and are indicated on the cladogram to facilitate the discussion. Also, there is one report of $x = 4$ for *Bradburia* that is not indicated on the cladogram.

Taxa *C. lanuginosa* (lan), *C. gossypina* subsp. *gossypina* f. *gossypina* (gs-gg), *C. gossypina* subsp. *hyssopifolia* (gs-h), and *C. linearifolia* subsp. *linearifolia* (li-l) are defined only by character conflicts and/or character losses and may be hybrids themselves or the parent with which another hybrid is not grouped. Two taxa *C. godfreyi* f. *viridis* (gd-v) and C. *gossypina* subsp. *cruiseana* (gs-c) are possible parents with which the hybrids are grouped because they have no autapomorphies

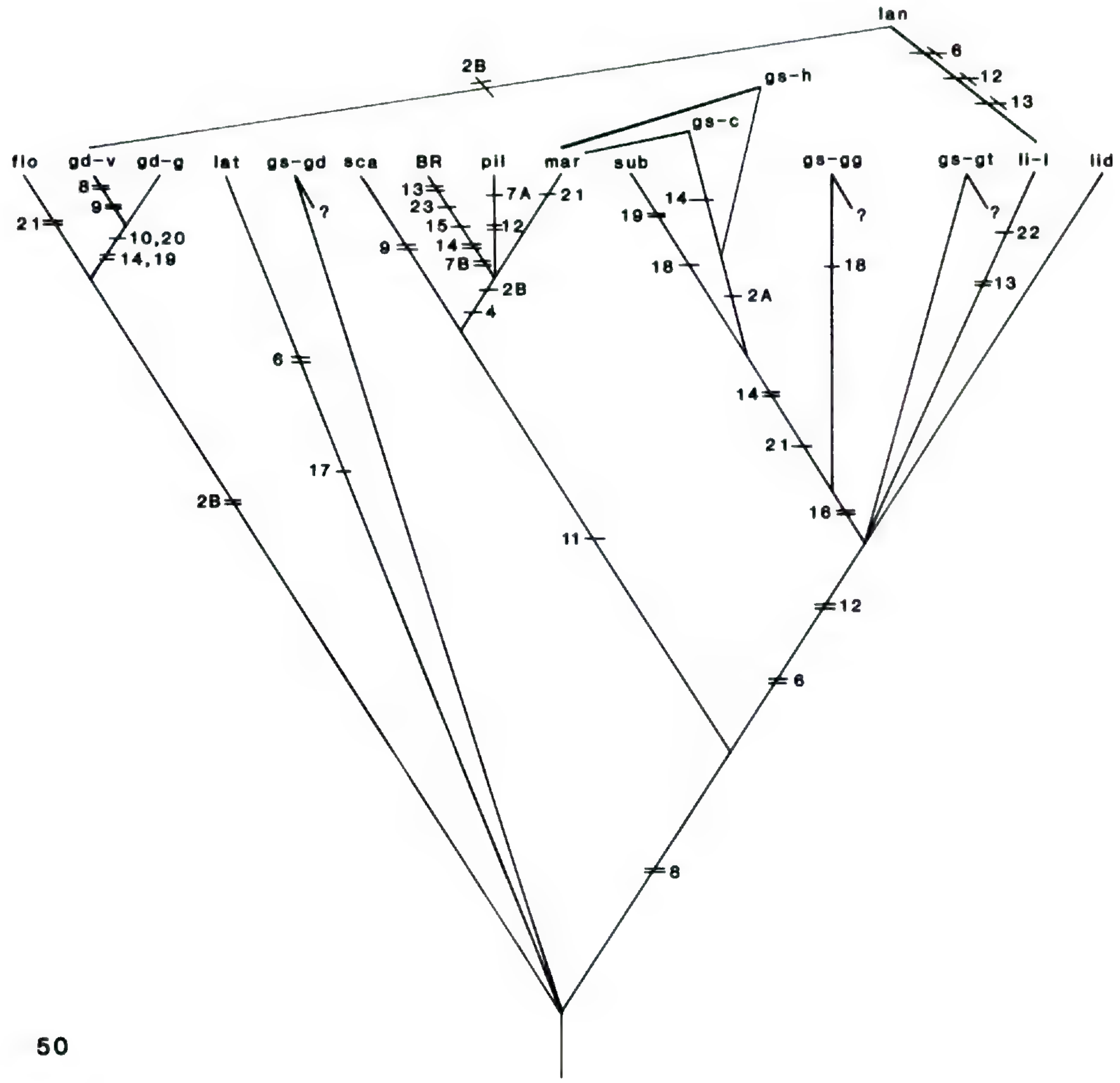


FIGURE 50. Cladogram of *Chrysopsis* and *Bradburia* with reticulations.

and have a single taxon as a sister taxa. If we construct hypotheses based on these data we obtain the following results: lan = gd-g × li-l, gs-c & h = sub × pil or mar, and gs-gg = sub × some taxon without 8. Because so many of the taxa are sympatric or parapatric, the distributions are not of much assistance in refining the hypotheses. The exceptions are *C. gossypina* subspp. *cruiseana* and *hyssopifolia* (gs-c & h) that can be attributed to a cross between *C. subulata* and *C. mariana* (sub × mar).

There are four taxa with no autapomorphies [gd-g (*C. godfreyi* f. *godfreyi*), gs-gd (*C. gossypina* subsp. *gossypina* f. *decumbens*), gs-gt, li-d)] that are potential hybrids or parents. Their chromosome numbers show that all of the gs taxa are $x = 9$, and based on outgroup comparison the base number for the genera is probably $x = 5$ (this agrees with Semple, 1981). Therefore, the subspecific taxa of *C. gossypina* are most likely hybrids. This supports the hypotheses of hybridization for three of the subspecific taxa of *C. gossypina* (gs-gg, gs-c & h), however *C. gossypina* f. *trichophylla* and f. *decumbens* (gs-gt, gs-gd) were not identified, except for noting that they lacked autapomorphies. The cladogram clearly indicates why *C. gossypina* f. *decumbens* was overlooked, it has no synapomorphies or autapomorphies. If it is a hybrid it is an excellent example of a hybrid inheriting all plesiomorphies of both parents and appearing in an ancestral position on the cladogram. Likewise, *C. gossypina* f. *trichophylla* was overlooked because it inherited most, but not all, of the plesiomorphies. The chromosome number of $x = 5$ does not support, and in fact falsifies, the hypothesis of hybridization for *C. lanuginosa* because one of the hypothesized parents has $x = 5$ and the other $x = 9$.

Figures 47–49 show that the $x = 9$ taxa do not

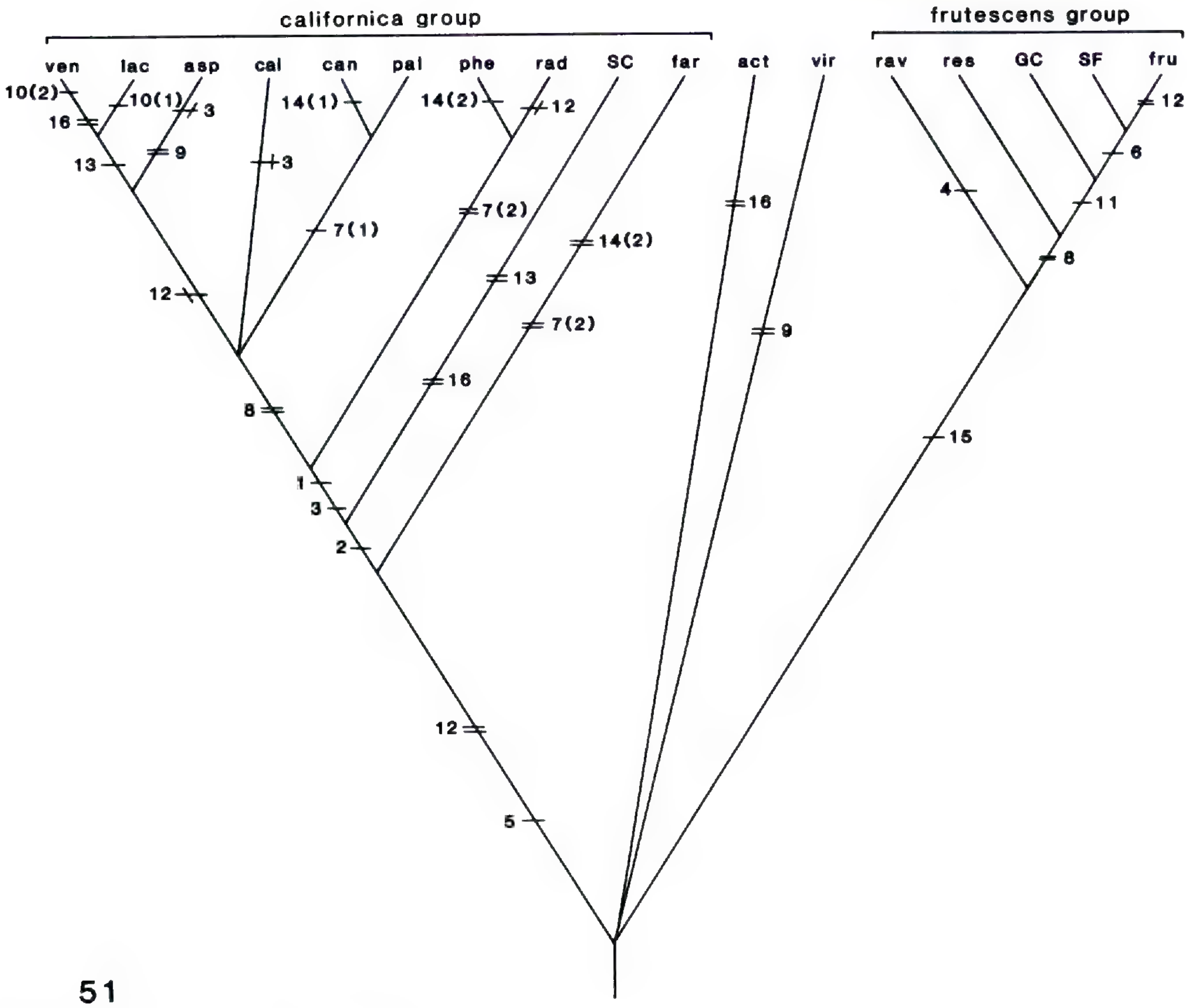


FIGURE 51. Cladogram of *Encelia*.

form a monophyletic group. Semple (1981) proposed that the $x = 9$ group is from one hybridization event between an individual of *C. subulata* and one of *C. mariana* with subsequent selections to give different combinations of parental genes. The cladogram does not support that statement because of the different combinations of characters in the five different subspecific taxa. However, it also does not reject Semple's suggestion. It simply suggests that one should also consider the possibility of several different hybridization events involving the same species as parents with different characters being inherited each time (Fig. 50).

Using cladistics alone has not given us a clear answer to the question of hybridization in *Chrysopsis* and *Bradburia,* however when the hypotheses of hybridization are tested with additional information, such as distribution and ploidy level, we have been able to make five putative hybrids and gain some insight into possible parents.

EXAMPLE 5. *ENCELIA* (ASTERACEAE) (CLARK, PERS. COMM.)

Encelia Adanson (Appendix Q) comprises 18 taxa distributed in the western United States. All taxa are diploids. The data matrix and the taxon distributions were furnished by Curtis Clark.

There are at least two cladograms that are equally parsimonious (Figs. 51, 52) and one that is one step longer (Fig. 53); all have different branching patterns. There are several additional cladograms that have slightly different character distributions but do not have different branching patterns, and these are not illustrated. On the three cladograms there are several taxa that change positions. *Encelia farinosa* can be placed as the sister taxa of *E. farinosa* var. *phenicodonta* (Figs. 52, 53) or near the base of the cladogram (Fig. 51). In either case it is only defined by character loss and/or homoplasy. Likewise *E. asperifolia* is either the sister taxon of *E. ventorum/E. laciniata* (Fig. 51) or it is near the basal node (Figs. 52, 53). In all three positions *E. asperifolia*

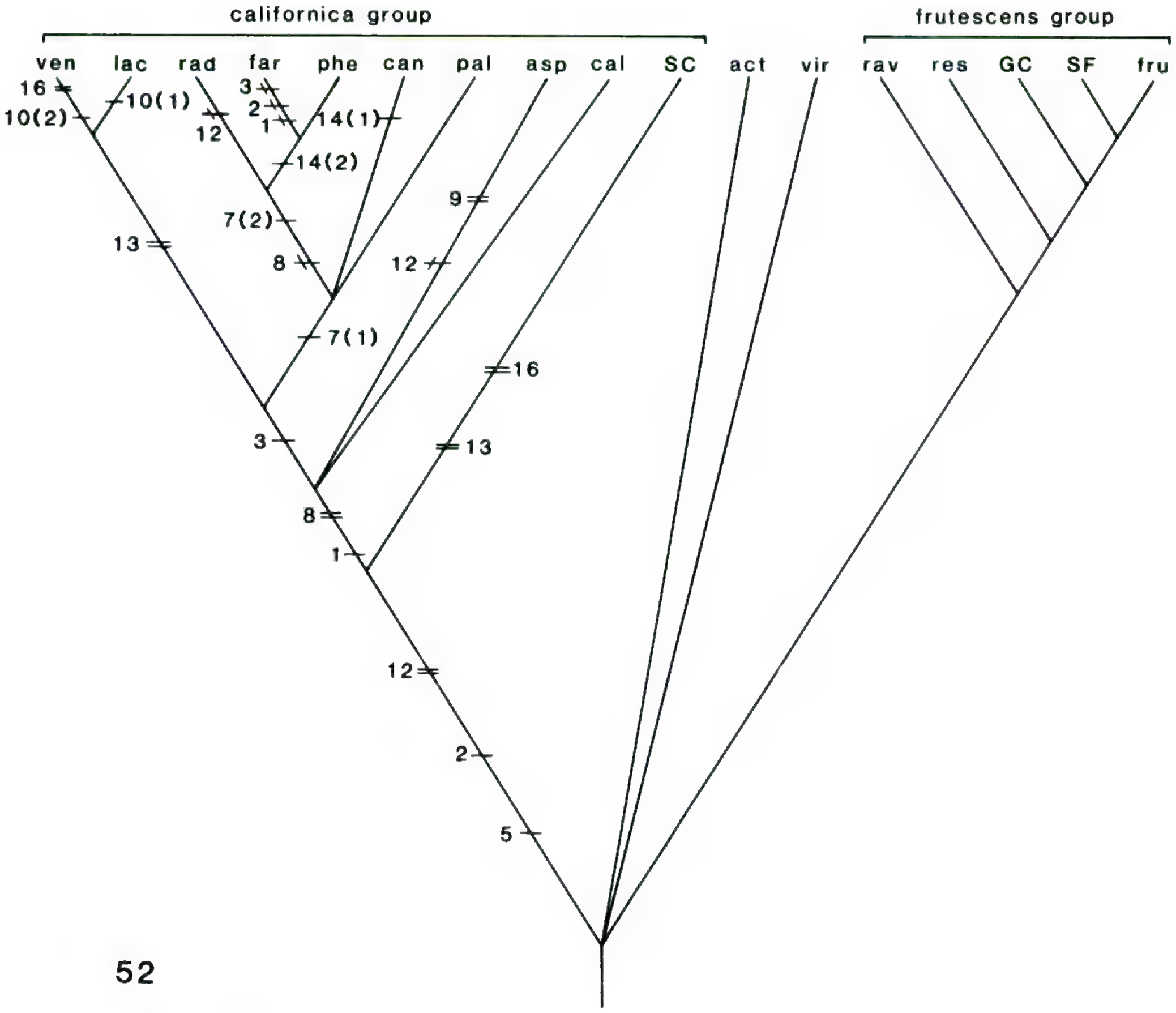


FIGURE 52. Cladogram of *Encelia*.

is identified by character loss and/or homoplasy. *Encelia canescens* is either the sister taxon of *E. palmeri* (Fig. 51) or it shares the node defined by character 7(1) with several other taxa (Figs. 52, 53). Two other taxa have some indication that they may be hybrids, *E. laciniata* with intermediate character 10(1) and the unidentified taxon from Santa Carla (SC) that is always defined by character homoplasy. There are three taxa that can be indicated as possibilities but cannot be placed as hybrids, ancestors, or parents because they have few apomorphies. Two taxa (*E. virginensis* and *E. actoni*) have only one apomorphy each and they appear on the cladogram at the basal node, and *E. californica* has a slight change in position depending on whether character 3 is treated as a character loss or not (Figs. 51–53).

Encelia farinosa and *E. asperifolia* stand out because of character losses and homoplasy. The best estimate for *E. farinosa* is that it is a hybrid between *E. farinosa* var. *phenicodonta* (its sister taxon in Figs. 52, 53) and something without characters 1, 2, and 3. *Encelia asperifolia* may be a hybrid between something without characters 3 and 12 (perhaps something in the "Frutescens group") and something in the "Californica group" with character 8 (perhaps *E. californica* with which it is closely grouped and whose lack of apomorphies may account for *E. asperifolia*'s similar situation). *Encelia canescens* might be a hybrid, between *E. palmeri* its sister taxon in Figure 51 and *E. farinosa* var. *phenicodonta,* because of the intermediate nature of character 14. *Encelia laciniata* may be a hybrid between *E. ventorum* and some other taxon that has not left a trace. If so, *E. laciniata* is an example of a hybrid inheriting all of the apomorphies of one parent. If the taxon from Santa Clara (SC) is a hybrid, one parent might be *E. ventorum* because of characters 13 and 16 and the other parent something from the "Californica group" that has character 12. A summation of possible hybrids is as follows: far = phe × some-

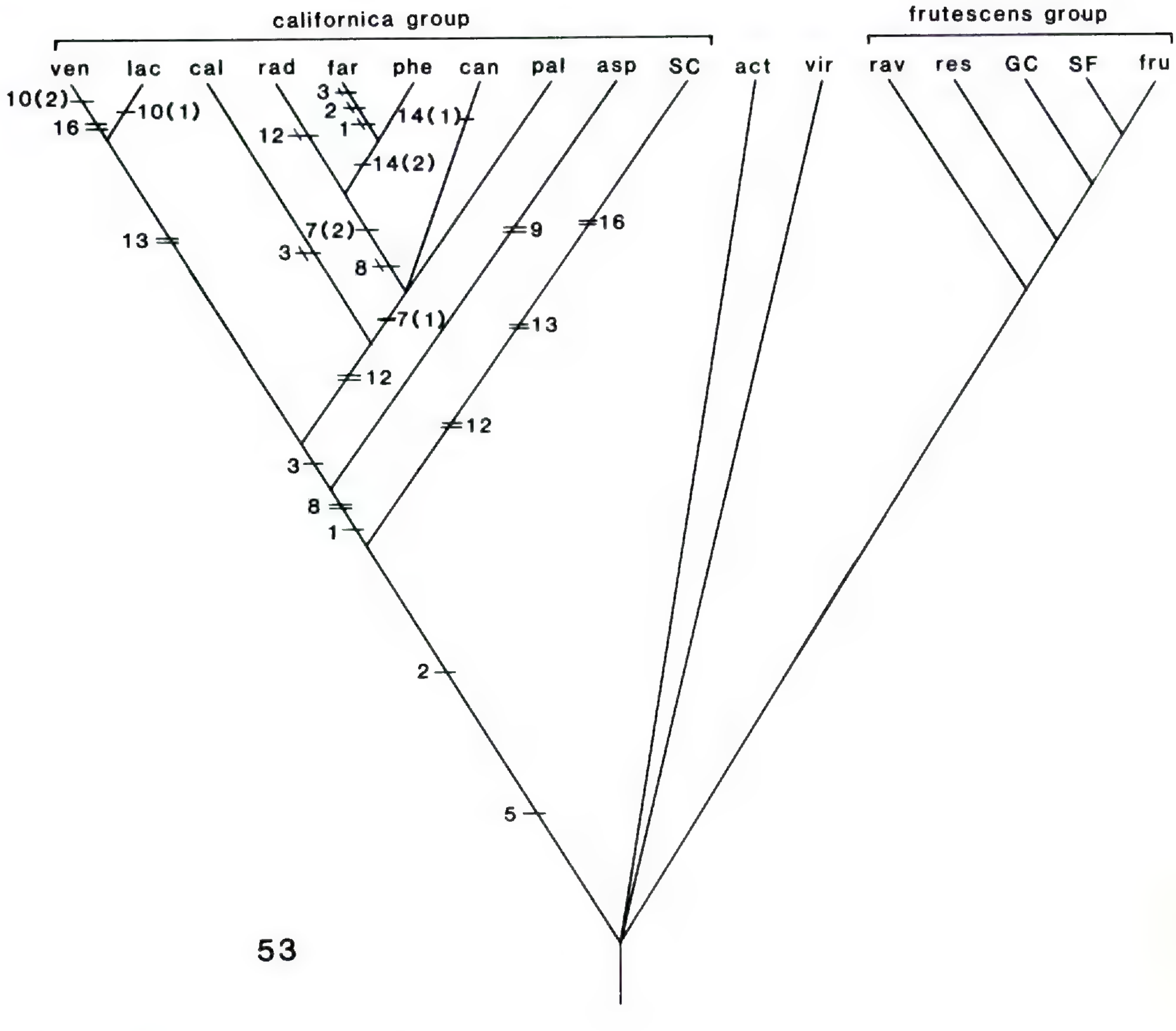


FIGURE 53. Cladogram of *Encelia*.

thing without 1, 2, and 3, asp = cal × something in the "Frutescens group" with 8, can = pal × phe, lac = ven × ?, and SC = ven × "Frutescens group" with 12.

Listed above are five hypotheses of hybridization and some possible parents. Examination of the distribution patterns and other data do not support two of the hypotheses (*E. farinosa* and SC) and an additional one is added. An F_1 that has been identified as *E. virginensis* has been found growing with *E. actoni* so that *E. virginensis* should be investigated as a possible hybrid with *E. actoni* as one of the parents.

Using the distributions we can narrow down the choice of possible parents to the following: asp = cal × SF, can = phe × pal, lac = ven × ?, and vir = act × ?.

The reticulate cladogram is illustrated in Figure 54. The hybrids indicated with solid lines are those that were supported as hybrids by both the cladistic analysis and the distributional data; those with dotted lines were supported by only one of the two.

EXAMPLE 6. *MONTANOA* (ASTERACEAE) (FUNK, 1982)

Montanoa Cerv. (Appendix R) has 20 species in Mexico and Central America and five in northern South America. Examining one of the equally parsimonious cladograms (Fig. 55), only one taxon (*M. hexagona*) shows any strong indication of hybridization. This taxon has the only two character losses on the cladogram. There are however, three known high level polyploids in the genus (Fig. 55). Two of these (*M. revealii* and *M. guatemalensis*) show no evidence of being hybrids. The third is *M. hexagona* and, it could be a hybrid between its sister taxon, *M. hibiscifolia,* and something outside of the group defined by character 34. None of the polyploids are sympatric with any other species and they all have at least 95% pollen viability, and during meiosis there is at least one stage where a complete bivalent can be observed. So, we are left with these three species being either very old polyploids, two of which have developed autapo-

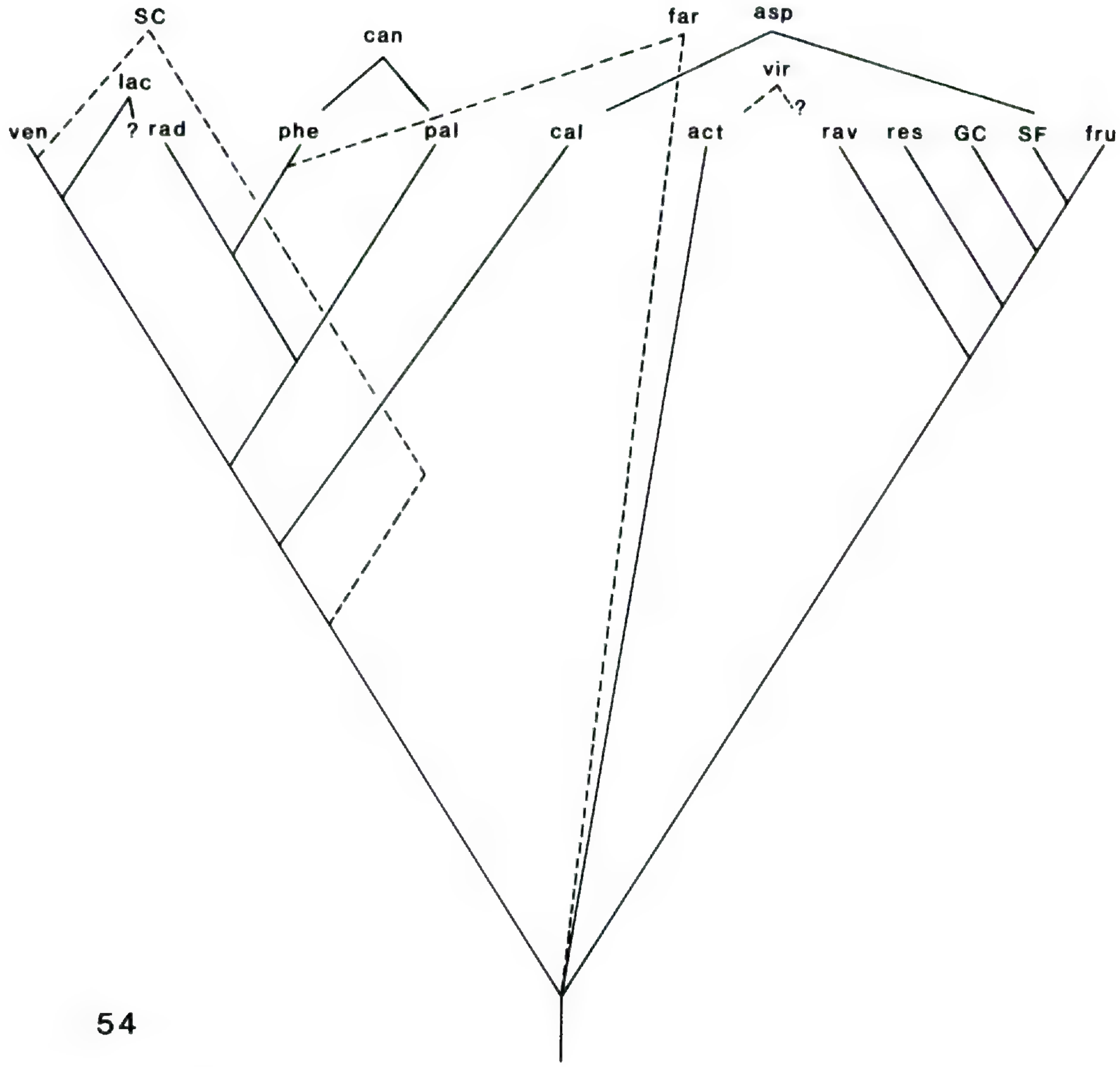


FIGURE 54. Cladogram of *Encelia* with reticulations.

morphies, or the parents are extinct so the relationships do not show up on the diagram. Or, less likely, they are autopolyploids with the diploids no longer extant. The cladogram cannot help us in resolving this matter.

EXAMPLE 7. *ACMELLA* (ASTERACEAE) (JANSEN, IN PRESS)

This last example presents the most difficult case: one where there are more hybrids than nonhybrids in a genus, where the hybrids are hybridizing, where there are few characters in the analysis and some of the hybrids have inherited mostly plesiomorphies, and where the hybrids are weeds that disperse readily and tend to hybridize wherever they are. Although not the rule, such situations are not that unusual in the Asteraceae family. One such genus is *Acmella* (Appendix S). The species of *Acmella* used to be part of *Spilanthes* Jacq. but were removed by Jansen (1981). There are 39 taxa (30 species), 16 of which are diploids (23 polyploids; ploidy level is estimated in some species, see Appendix S). The genus is pantropical with one species in the southeast United States. Some species form autopolyploid series that would allow them to cross with allopolyploids. Also, some reproduce asexually so odd level polyploids persist in nature.

There are at least ten equally parsimonious cladograms of *Acmella* and a large number (over 100) that are only a few steps longer. Many of these cladograms have very different structures. I have selected one to discuss as a representative (Fig. 56), but in no way am I indicating that this particular cladogram is to be preferred over any other. In Figure 56 there are only three apomorphies (excluding autapomorphies) that are not either subsequently lost or found elsewhere on the cladogram [7, 1, 2(2)]. The three major

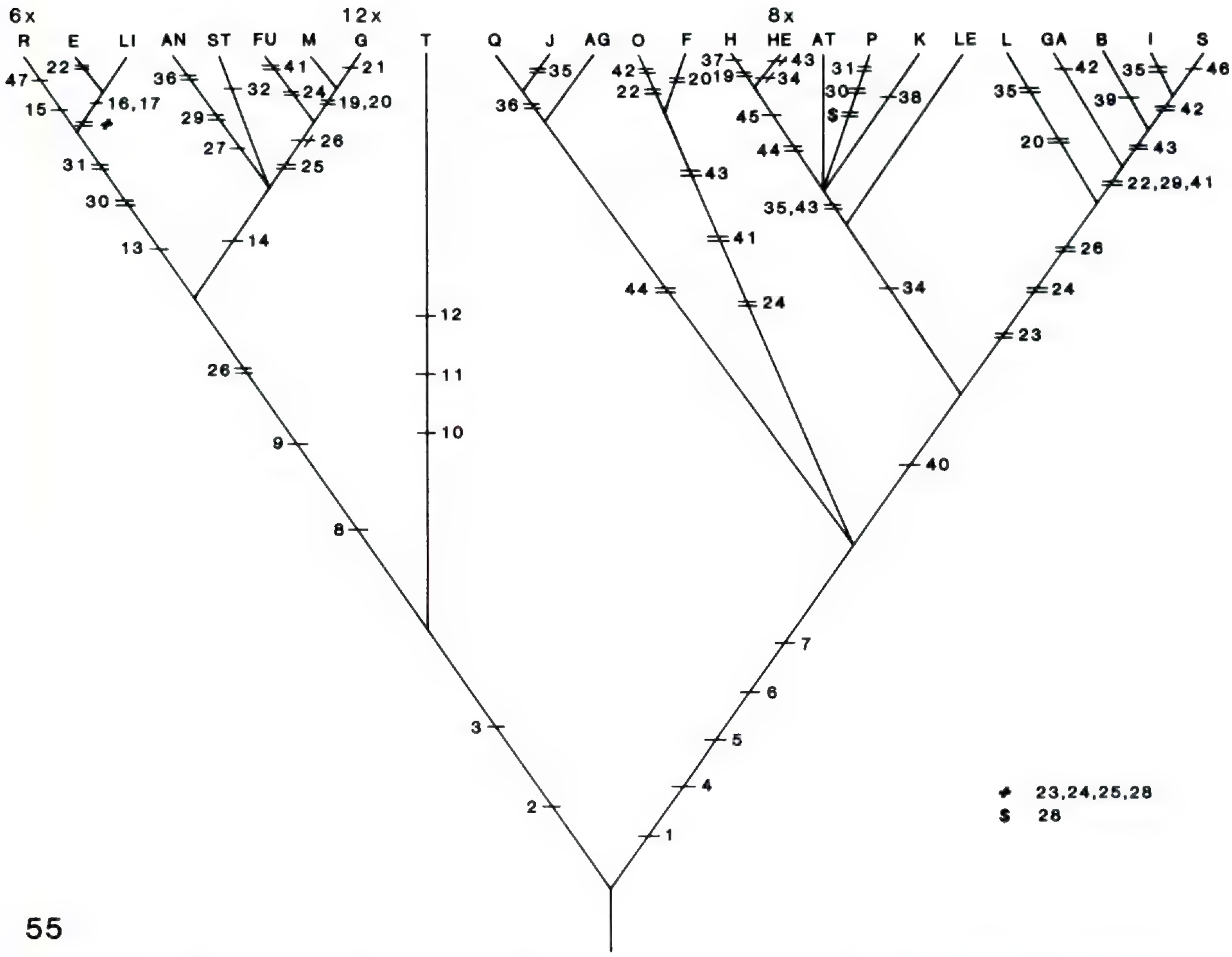


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FIGURE 55. Cladogram of *Montanoa,* numbers above taxa indicate ploidy level of known polyploids.

groups of Jansen (in press; indicated in Fig. 56 by the large numbers 1, 2, and 3) are obvious on the cladogram and only one, number 2, is non-monophyletic (this group was non-monophyletic on all of the cladograms that I constructed). Some taxa may be hybrids between the three major groups, some of the more obvious ones are as follows:

1. *A. decumbens* var. *decumbens* (23a) may be a hybrid between some taxon in group 1 and one in group 2 because it has apomorphies 1 and 2.

2. *A. poliolepidica* (1) may be a hybrid between a taxon in group 1 that has apomorphy 20 and a taxon in group 3 with apomorphy 16.

3. The ancestor of *A. darwinii* (7) and *A. sodiroi* (8) may have been a hybrid between a taxon in group 2 and one in group 3 that has apomorphies 18(2) and 17(2).

4. *A. paniculata* (19) may be the hybrid of a taxon in group 3 and one outside of it because of its lack of apomorphy 22 (only two taxa in group 3 lack apomorphy 22).

Other taxa show some indication of hybridization within the groups. However, there is no strong indication of hybrids and their parents within the groups because there are so many alternative groupings and so few characters. Some taxa are obviously hybrids or of hybrid ancestry because of their ploidy level (Fig. 56, Appendix S) but there is little indication of what their history might be. The different parsimony cladograms give us different possible hybrids and parents. With the exception of two or three small groups of species that appear repeatedly on many, if not all, of the cladograms there are a few additional questions, such as biogeography, character evolution, or ecology that can be investigated using these cladograms. To a large extent we are dealing with straight character patterns.

We have apparently reached the limits of cladistics with genera such as *Acmella.* I say this because cladistics is merely an organized way of looking at the relevant data that have been gathered. If no consistent pattern develops using cladistics then the data are responsible, not the

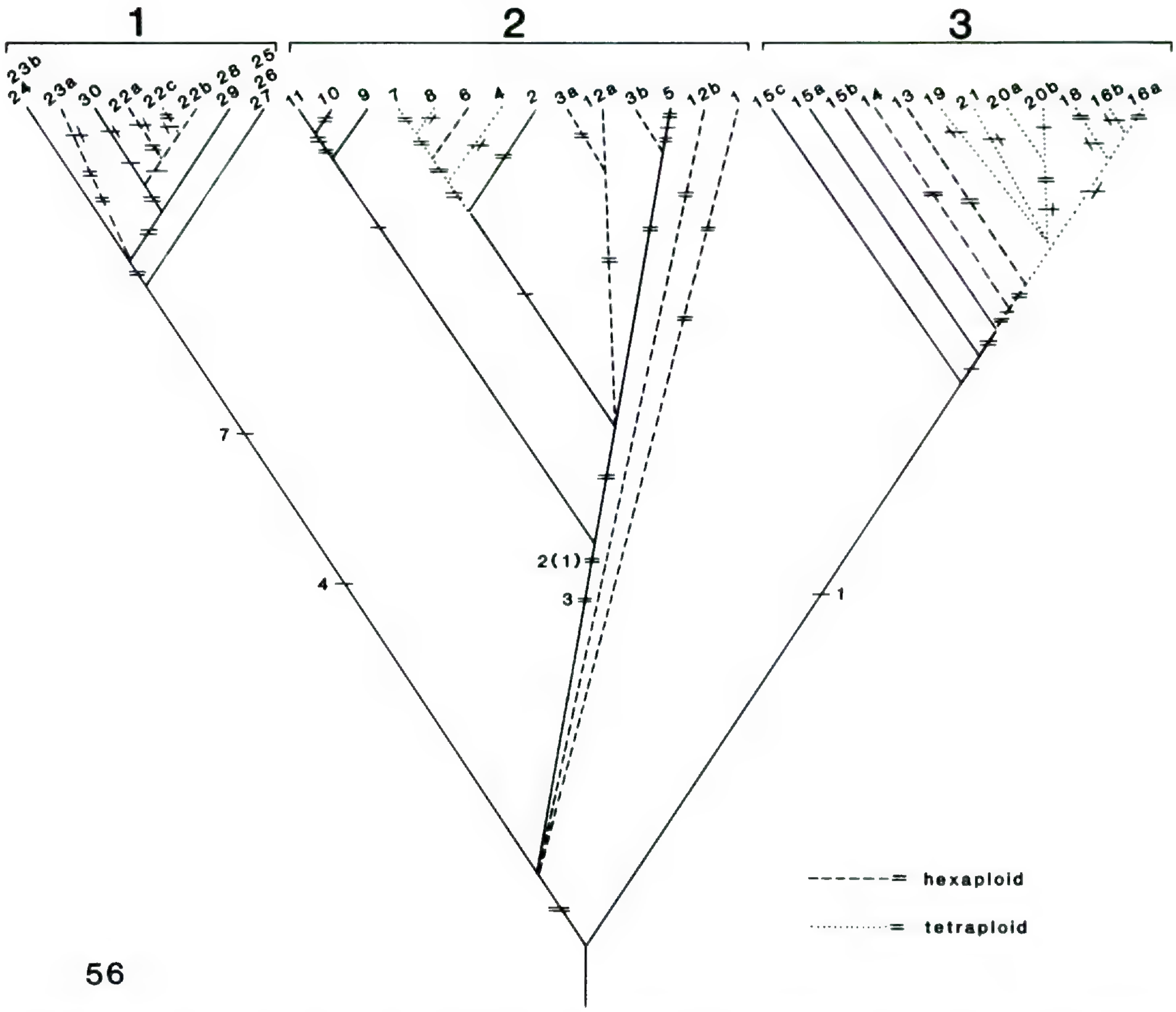

FIGURE 56. One of the many equally parsimonious cladograms for *Acmella,* many of which have different topologies.

method. So the lack of resolution in genera such as *Acmella* is simply a reflection of the data. In the future we may be able to gain more information from genetic level research to increase the data base and obtain further resolution from cladistic analyses.

CLASSIFICATION OF HYBRIDS

A number of papers have been published that discuss the possibilities of classifying hybrids (Wiley, 1979; Wagner, 1980; Humphries, 1983; Humphries & Funk, 1984; Nelson, 1973) so the alternatives need not be discussed in this paper. As discussed in Humphries and Funk (1984), I prefer the method called phyletic sequencing or the annotated Linnean Hierarchy. This method works on the basic principle that all information from a cladogram is available in a classification and that a cladogram can be reconstituted from a classification. In such a classification only monophyletic groups are recognized. An example using the genus *Anacyclus* from Figure 39 is listed below:

Classification of *Anacyclus* without hybrids
- *Anacyclus*
  - *A. pyrethrum*
  - *A. monanthos*
  - *A. maroccanus*
  - *A. radiatus*
  - Clavatus species group
    - *A. linearilobus*
    - *A. clavatus*
    - *A. homogamos*
  - *A. latealatus*
  - *A. nigellifolius*

The hybrids can be added in several ways; one

is to make them the sister taxon of either one of the parents. Using the first parent in the phyletic sequence we arrive at the following classification:

Classification of *Anacyclus* with hybrids
- *Anacyclus*
  - Sect. *Pyrethraria*
    - *A. pyrethrum*
    - +*A. officinarum* sedis mutabilis (*A. pyrethrum* × *radiatus*)
  - Sect. *Anacyclus*
    - *A. monanthos*
    - *A. maroccanus*
    - *A. radiatus*
    - Clavatus species group
      - *A. linearilobus*
      - *A. homogamos*
      - +*A. inconstans* sedis mutabilis (*A. homogamos* × *clavatus*)
      - +*A. valentinus* sedis mutabilis (*A. monogamos* × *clavatus*)
      - *A. clavatus*
    - *A. latealatus*
    - *A. nigellifolius*

The special notations include a plus sign (+) for hybrids, the parental species listed are the hybrids in parentheses, and the latin phrase sedis mutabilis ("changeable position") that is used to mean a polytomy in the cladogram. The cladogram is recovered in the following manner. Section *Pyrethraria* is the sister group of sect. *Anacyclus,* and *A. pyrethrum* and *A. officinarum* are sister taxa within sect. *Pyrethraria* (Fig. 39). In succession; *A. monanthos* is the sister taxon of the remaining species; *A. marocannus* is the sister taxon to the remaining species; *A. radiatus* is the sister taxon to the remaining species; the "clavatus group" is the sister group to *A. latealatus* and *A. nigellifolius* (Fig. 39); within the "clavatus group," *A. linearilobus* is the sister taxa of *A. clavatus* and *A. homogamos* and their two hybrids; and *A. homogamos* is the sister taxon of *A. clavatus,* but forms a polytomy with the two hybrids.

I add to this the provision that should the two parents occur in different subgeneric groups (or different genera) then the hybrid should be listed in both groups.

Conclusion

In general, phylogenetic systematics can be used to help identify possible hybrids and their parents for further study. However, several conditions exist in some groups that make a cladistic analysis more difficult. Such conditions include the following: 1) having an increased percentage of species within a group that are hybrids, 2) having hybrids that have mainly plesiomorphies, 3) having hybrids that hybridize with one another, 4) having species that can reproduce asexually, and/or 5) having introgression occur.

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APPENDICES A–S. Only the apomorphies are indicated in the data matrices because in phylogenetic systematics only the apomorphies are used to group taxa.

APPENDIX A. Data matrix for Figure 2.

	Apomorphies						
Taxa	1	2	3	4	5	6	7
A	1		1		1	1	1
B	1		1	1	1	1	1
C	1		1	1			
D	1	1					
E	1						

APPENDIX B. Data matrix for Figures 3–6.

	Apomorphies				
Taxa	1	2	3	4	5
A	1		1		1
B	1		1	1	
C	1	1			
H	1			1	1

APPENDIX C. Data matrix for Figure 7.

	Apomorphies					
Taxa	1	2	3	4	5	6
A	1		1		1	1
B	1		1	1		
C	1	1				
H	1		1	1	1	1

APPENDIX D. Data matrix for Figures 8–12.

Taxa	Apomorphies				
	1	2	3	4	5
A		1	1		1
B	1		1		1
C				1	1
H1	1	1	1		1
H2	1	1	1		1

APPENDIX E. Data matrix for Figure 13.

Taxa	Apomorphies				
	1	2	3	4	5
A	1		1		1
B		1	1		1
C				1	1
H			1		1

APPENDIX F. Data matrix for Figures 14–17, 19.

Taxa	Apomorphies								
	1	2	3	4	5	6	7	8	9
A	1	1							1
B	1		1	1					1
C	1		1		1				1
D						1	1		1
E						1		1	1
H	1		1		1	1	1		1

APPENDIX G. Data matrix for Figure 18.

Taxa	Apomorphies								
	1	2	3	4	5	6	7	8	9
A	1	1							1
B	1		1	1					1
C	1		1		1				1
D						1	1		1
E						1		1	1
H									1

APPENDIX H. Data matrix for Figures 20–22.

Taxa	Apomorphies				
	1	2	3	4	5
A	1	1	1		1
B	1	1	1	1	1
C	1			1	1
D					1

APPENDIX I. Data matrix for Figures 23–25.

Taxa	Apomorphies											
	1	2	3	4	5	6	7	8	9	10	11	12
A	1										1	1
B	1	1										
C	1	1	1									
D	1	1	1	1						1		
E	1	1	1	1	1							
F	1	1	1	1	1	1		1				
G	1	1	1	1	1	1	1		1			
H	1	1	1	1	1	1	1	1	1			
I	1	1	1	1						1	1	1

APPENDIX J. *Microloma* R. Br. (Asclepidaceae). Abbreviations.—A. *M. incanum* Decne.—B. *M. longitubum* Schlechter.—C. *M. burchellii* N. E. Brown.—D. *M. armatum.*—E. *M. campanulatum.*—F. *M. dolichanthum.*—G. *M. spinosum* N. E. Brown.—H. *M. viridiflorum* N. E. Brown.—I. *M. lanatum.* Characters.—Data published in Bremer and Wanntorp (1979) and Humphries (1983) but no character list was furnished in either publication. Data matrix.—For Figures 26, 27, 36–38.

Taxa	Apomorphies						
	1	2	3	4	5	6	7
A							1
B	1					1	1
C	1	1	1	1	1	1	1
D		1	1	1	1	1	1
E			1	1	1	1	1
F				1	1	1	1
G				1	1	1	1
H					1	1	1
I					1	1	1

APPENDIX K. Data matrix for Figures 28, 29.

Taxa	Apomorphies												
	1	2	3	4	5	6	7	8	9	10	11	12	13
A	1	1		1		1		1					
B	1	1		1		1	1						
C	1	1		1	1								
D	1	1	1										
E	1								1	1			
F	1								1		1	1	
G	1								1		1		1
H	1	1					1					1	

APPENDIX L. Data matrix for Figures 30, 31.

	Apomorphies								
Taxa	1	2	3	4	5	6	7	8	9
A	1	1							1
B	1		1	1					1
C	1		1		1				1
D						1	1		1
E						1		1	1
H	1				1	1	1		1

APPENDIX M. Data matrix for Figures 32, 33.

	Apomorphies												
Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13
A	1	1	1	1	1	1							1
B	1	1	1	1	1		1						1
C	1	1	1	1				1	1				1
D										1	1		1
E										1		1	1
H	1	1		1					1		1		1

APPENDIX N. *Anacyclus* L. (Asteraceae, Anthemideae). Abbreviations.—A. *A. pyrethrum* (L.) Link var. *pyrethrum*.—B. *A. pyrethrum* (L.) Link var. *depressus* (Ball) Maire.—C. *A. monanthos* (L.) Thell.—D. *A. maroccanus* (Ball) Ball.—E. *A. radiatus* Loisel.—F. *A. coronatus* (Murb.) Humphries.—G. *A. clavatus* (Desf.) Pers.—H. *A. homogamos* (Maire) Humphries.—I. *A. valentinus* L.—J. *A. inconstans* Pomel.—K. *A. linearilobus* Boiss. & Reuter.—L. *A. latealatus* Hub.-Mor.—M. *A. nigellifolius* Boiss.—N. *A. officinarum* Hayne. Characters.—Published in Humphries (1979). Data matrix.—Lower case letters represent groups of characters that display that pattern so that there are five apomorphies that have the distribution patterns of *a*, etc. For Figures 39–43.

	Apomorphies																
Taxa	a (5)	b (3)	c (1)	d (3)	e (3)	f (1)	g (3)	h (1)	i (1)	j (1)	k (1)	l (1)	m (3)	n (5)	o (4)	p (1)	q (1)
AB	1													1	1	1	1
C	1	1	1													1	1
D	1	1	1	1													
EF	1	1	1	1	1	1				1							
G	1	1	1	1	1	1	1	1	1			1					
H	1	1	1	1	1	1	1	1	1		1						
I	1	1	1	1	1	1	1	1	1		1	1					
J	1	1	1	1	1	1	1	1	1		1	1					
K	1	1	1	1	1	1	1	1									
LM	1	1	1	1	1	1	1						1				
N	1	1				1									1		1

APPENDIX O. *Agastache* Clayt. (Lamiaceae). Abbreviations.—aur. *A. aurantiaca* (A. Gray) Lint & Epling.—brv. *A. breviflora* (A. Gray) Epling.—can. *A. cana* (W. J. Hooker) Wooton & Standley.—coc. *A. coccinea* (Greene) Lint & Epling.—epl. *A. eplingiana* R. Sanders.—mex. *A. mexicana* (H.B.K.) Lint & Epling.—mic. *A. micrantha* (A. Gray) Wooton & Standley.—mrn. *A. mearnsii* Wooton & Standley.—ne-h. *A. pallidiflora* (Heller) Rydberg subsp. *neomexicana* (Briquet) Lint & Epling var. *havardii* (A. Gray) R. Sanders.—ne-n. *A. pallidiflora* (Heller) Rydberg subsp. *neomexicana* (Briquet) Lint & Epling var. *neomexicana*.—pd-c. *A. pallida* (Lindley) Cory var. *coriacea* R. Sanders.—pd-p. *A. pallida* (Lindley) Cory var. *pallida*.—pf-r. *A. pallidiflora* (Heller) Rydberg subsp. *pallidiflora* var. *greenei* (Briquet) R. Sanders.—pf-i. *A. pallidiflora* (Heller) Rydberg subsp. *pallidiflora* var. *gilensis* R. Sanders.—pf-p. *A. pallidiflora* (Heller) Rydberg subsp. *pallidiflora* var. *pallidiflora*.—plm. *A. palmeri* (B. L. Robinson) Lint & Epling.—prn. *A. pringlei* (Briquet) Lint & Epling.—rup. *A. rupestris* (Greene) Standley.—wrt. *A. wrightii* (Greenmax) Wooton & Standley. Characters.—As published in Sanders (1981) except for the removal of apomorphy 7 because it was an autapomorphy for a subspecific taxon not used in this analysis. Data matrix.—For Figures 44–46.

	Apomorphies																																
Taxa	1	2	3	4	5	6	8	9	10	11	12	13	14	16	17	18	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36
aur	1		1		2				1	2				1				2′		1		1	1	1[a]									
brv										1[a]	1	1		1				1															
can	1	1	1		2′				1					1				2′		1									1				
coc										1				1				1′											1				
epl					1					1				1	1		1	1	1										1				
mex					1					1				1	1		1	1				1	1		1′								
mic				1		1															1												
mrn											1	1		1				1′												1			
ne-h							1					1	1	1				1			1									1			
ne-n							1					1		1				1			1												
pd-c														1		1		1															
pd-p									1	1				1		1		1												1		1	
pf-i								1				1′		1				1												1	1		
pf-p								1				1		1				1			1									1		1	
pf-r								1				1		1				1			1							1	1				1
plm										1				1	1			1				1	1[a]										
prn				1		1				1[a]		1		1				1			1												
rup	1	1	1		2″				1	2				1				2		1													
wrt																					1	1	1	1		1	1						

[a] Varies between the apomorphy and plesiomorphy.

APPENDIX P. *Chrysopsis* (Nutt.) Ell. and *Bradburia* Semple & Chinnappa (Asteraceae). Abbreviations.—BR. *B. hirtella* T. & G.—flo. *C. floridana* Small.—gd-g. *C. godfreyi* Semple f. *godfreyi.*—gd-v. *C. godfreyi* Semple f. *viridis* Semple.—gs-c. *C. gossypina* (Michx.) Elliot subsp. *cruiseana* (Dress) Semple.—gs-gd. *C. gossypina* (Michx.) Elliot subsp. *gossypina* f. *decumbens* (Chapm.) Godfrey.—gs-gg. *C. gossypina* (Michx.) Elliot subsp. *gossypina* f. *gossypina.*—gs-gt. *C. gossypina* (Michx.) Elliot subsp. *gossypina* f. *trichophylla* (Nutt.) Semple.—gs-h. *C. gossypina* (Michx.) Elliot subsp. *hyssopifolia* (Nutt). Semple.—lan. *C. lanuginosa* Small.—lat. *C. latisquamea* Pollard.—li-d. *C. linearifolia* Semple subsp. *dressii* Semple.—li-l. *C. linearifolia* Semple subsp. *linearifolia.*—mar. *C. mariana* (L.) Elliot.—pil. *C. pilosa* Nutt.—sca. *C. scabrella* T. & G.—sub. *C. subulata* Small. Characters—Original characters furnished by Semple and modified slightly by Funk.

	Transformation Series	Plesiomorphic Character	Apomorphic Character
2A.	Growth form	biennial	perennial
2B.	Growth form	biennial	annual
4.	Pubescence of basal rosettes	wooly	pilose
6.	Achene body	no translucent ribs	translucent ribs
7A.	Outer pappus	bristles narrow	bristles broad
7B.	Outer pappus	present	absent
8.	Upper cauline leaves	wooly	not wooly
9.	Glandulation of upper cauline leaves	sparsely	densely
10.	Upper leaf base	sessile, nonclasping	clasping
11.	Upper leaf size	not greatly reduced	greatly reduced
12.	Glandulation of peduncles	glandular	eglandular
13.	Upper leaf shape	elliptic	linear
14.	Upper leaf apex	obtuse	acute
15.	Glandulation of phyllaries	densely	eglandular
16.	Pubescence of phyllaries	glabrate	pubescent
17.	Phyllary size	narrow	broad
18.	Phyllary apex	acute-attenuate	long, subulate
19.	Outer phyllary size	much shorter than inner phyllaries	similar in size
20.	Head orientation in bud	erect	nodding
21.	Inflorescence type	open cymose	subumbellate
22.	Heads/inflorescence branch	few	many
23.	Disc florets	hemaphroditic	staminate

Data matrix.—For Figures 47–50.

	Apomorphies																					
Taxa	2A	2B	4	5	6	7A	7B	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
BR		1	1	1			1	1			1		1	1	1								1
flo		1																			1		
gd-g		1								1				1					1	1			
gd-v		1						1	1	1				1					1	1			
gs-c	1				1			1				1			1						1		
gs-gd																							
gs-gg					1							1			1	1							
gs-gt					1			1				1			1								
gs-h	1		1		1			1				1		1	1						1		
lan								1	1	1				1					1	1			1
lat					1												1						
li-d					1			1				1			1								
li-l					1			1				1	1		1								1
mar		1	1	1				1			1										1		
pil		1	1	1		1		1			1	1											
sca								1	1		1												
sub					1			1				1		1	1	1		1	1		1		

APPENDIX Q. *Encelia* Adanson (Asteraceae). Abbreviations.—act. *E. actoni* Elmer.—asp. *E. asperifolia* (S. F. Blake) Clark & Kyhas.—cal. *E. californica* Nutt.—can. *E. canescens* Cav.—far. *E. farinosa* Gray.—fru. *E. frutescens* Gray.—GC. Undescribed taxon from Grand Canyon (C. Clark, pers. comm.).—lac. *E. laciniata* Vasey & Rose.—pal. *E. palmeri* Vasey & Rose.—phe. *E. farinosa* Gray var. *phenicodonta* I. M. Johnston.—rad. *E. radians* Brandegee.—rav. *E. ravenii* Wiggins.—res. *E. resinosa* Brandegee.—SC. Undescribed taxon from Picachos de Santa Clara, Baja (C. Clark, pers. comm.).—SF. Undescribed taxon from San Felipe (C. Clark, pers. comm.).—ven. *E. ventorum* Brandegee.—vir. *E. virginensis* Nelson. Characters.—To be published by Clark (pers. comm.). Data matrix.—For Figures 51–54.

	Apomorphies															
Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
act																1
asp	1	1			1			1	1							
cal	1	1			1			1				1				
can	1	1	1		1		1	1				1		1		
GC								1			1				1	
far					1		2[a]					1		2		
fru						1		1			1	1			1	
lac	1	1	1		1			1		1			1			
pal	1	1	1		1		1	1				1				
phe	1	1	1		1		2[a]					1		2		
rad	1	1	1		1		2[a]									
rav				1											1	
res								1							1	
SC		1			1							1	1			1
SF						1		1			1				1	
ven	1	1	1		1			1		2			1			1
vir									1							

[a] Varies between apomorphies 2 and 1.

APPENDIX R. *Montanoa* Cerv. (Asteraceae). Abbreviations.—AN. *M. andersonii* McVaugh.—AG. *M. angulata* Badillo.—AT. *M. atriplicifolia* (Pers.) Sch. Bip.—B. *M. bipinnatifida* (Kunth) K. Koch.—E. *M. echinacea* S. F. Blake.—F. *M. fragrans* Badillo.—FU. *M. frutescens* DC.—GA. *M. grandiflora* DC.—G. *M. guatemalensis* Robins. & Greenm.—HE. *M. hexagona* Robins. & Greenm.—H. *M. hibiscifolia* Benth.—I. *M. imbricata* V. A. Funk.—J. *M. josei* V. A. Funk.—K. *M. karwinskii* DC.—L. *M. laskowskii* McVaugh.—LE. *M. leucantha* (Lag.) S. F. Blake.—LI. *M. liebmannii* (Sch. Bip.) S. F. Blake.—M. *M. mollissima* Groenland.—O. *M. ovalifolia* DC.—P. *M. pteropoda* S. F. Blake.—Q. *M. quadrangularis* Sch. Bip.—R. *M. revealii* H. Robinson.—S. *M. speciosa* DC.—ST. *M. standleyi* V. A. Funk.—T. *M. tomentosa* Cerv. Characters.—Published in Funk (1982). Data matrix.—For Figure 55.

Taxa	Apomorphies																				
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	19	20	21	22
AN		1	1					1	1					1							
AG	1			1	1	1	1														
AT	1			1	1	1	1														
B	1			1	1	1	1														1
E		1	1					1	1				1			1	1				1
F	1			1	1	1	1												1		
FU		1	1					1	1					1							
GA	1			1	1	1	1														1
G		1	1					1	1					1				1	1	1	
HE	1			1	1	1	1														
H	1			1	1	1	1											1			
I	1			1	1	1	1														1
J	1			1	1	1	1														
K	1			1	1	1	1														
L	1			1	1	1	1												1		
LE	1			1	1	1	1														
LI		1	1					1	1				1			1	1				
M		1	1					1	1					1				1	1		
O	1			1	1	1	1														1
P	1			1	1	1	1														
Q	1			1	1	1	1														
R		1	1					1	1				1		1						
S	1			1	1	1	1														1
ST		1	1					1	1					1							
T		1	1							1	1	1									

APPENDIX R. Continued.

Apomorphies																							
23	24	25	26	27	28	29	30	31	32	34	35	36	37	38	39	40	41	42	43	44	45	46	47
			1	1		1						1											
																				1			
										1	1					1			1				
1	1		1			1									1	1	1			1			
1	1	1	1		1		1	1															
	1																1		1				
		1																					
1	1		1			1										1	1	1					
		1																					
											1					1				1	1			
										1	1		1			1			1	1	1			
1	1		1			1					1					1	1	1	1				
											1	1								1				
										1	1			1		1							
1	1		1								1					1							
										1						1							
1	1	1	1		1		1	1															
		1																					
	1																1	1	1				
					1		1	1		1	1					1			1				
												1								1			
			1				1	1															1
1	1		1			1										1	1	1	1			1	
			1						1														

APPENDIX S. *Acmella* Rich. ex Pers. (Asteraceae). Abbreviations (* indicates chromosome number is an estimate from pollen diameter).—1. *A. poliolepidica* (A. H. Moore) R. K. Jansen (4*x*).—2. *A. pilosa* R. K. Jansen (2*x*).—3a. *A. oppositifolia* Rich. var. *repens* (Walt.) R. K. Jansen (4*x*).—3b. *A. oppositifolia* Rich. var. *oppositifolia* (2*x*, 3*x*, 4*x*, 5*x*, 6*x*).—4. *A. ciliata* (H.B.K.) Cass. (6*x*).—5. *A. caulirhiza* Delile (2*x*).—6. *A. calva* (DC.) R. K. Jansen (4*x**).—7. *A. darwinii* (D. M. Porter) R. K. Jansen (6*x**).—8. *A. sodiroi* (Hieron) R. K. Jansen (6*x*).—9. *A. ramosa* (Hensl.) R. K. Jansen. (2*x*).—10. *A. pusilla* (Hook. & Arn.) R. K. Jansen (2*x*, 4*x*).—11. *A. lundellii* R. K. Jansen (2*x**).—12a. *A. papposa* (Hemsl.) R. K. Jansen var. *papposa* (4*x*).—12b. *A. papposa* (Hensl.) R. K. Jansen var. *macrophylla* (Greenm.) R. K. Jansen (4*x*).—13. *A. iodiscaea* (A. H. Moore) R. K. Jansen (4*x*).—14. *A. uliginosa* (Sw.) Cass. (4*x*).—15a. *A. filipes* (Greenm.) R. K. Jansen var. *filipes* (2*x**).—15b. *A. filipes* (Greenm.) R. K. Jansen var. *cayensis* R. K. Jansen (2*x**).—15c. *A. filipes* (Greenm.) R. K. Jansen var. *parvifolia* (Benth.) R. K. Jansen (2*x*).—16a. *A. alba* (L'Herit.) R. K. Jansen var. *alba* (6*x**).—16b. *A. alba* (L'Herit.) R. K. Jansen var. *ecuadorensis* R. K. Jansen (6*x**).—18. *A. leucantha* (H.B.K.) R. K. Jansen (6*x**).—19. *A. paniculata* (DC.) R. K. Jansen (4*x**).—20a. *A. radicans* (Jacq.) R. K. Jansen var. *radicans* (6*x*).—20b. *A. radicans* (Jacq.) R. K. Jansen var. *devilis* (H.B.K.) R. K. Jansen (6*x*).—21. *A. brachyglossa* Cass. (6*x*).—22a. *A. grandiflora* (Turcz.) R. K. Jansen var. *grandiflora* (4*x**).—22b. *A. grandiflora* (Turcz.) R. K. Jansen var. *brachyglossa* (Benth.) R. K. Jansen (4*x*).—22c. *A. grandiflora* (Turcz.) R. K. Jansen var. *discoidea* R. K. Jansen (6*x**).—23a. *A. decumbens* (Smith) R. K. Jansen var. *decumbens* (4*x*).—23b. *A. decumbens* (Smith) R. K. Jansen var. *affinis* (Hook. & Arn.) R. K. Jansen (2*x*).—24. *A. leptophylla* (DC.) R. K. Jansen (2*x*).—25. *A. bellidioides* (Smith) R. K. Jansen (2*x*).—26. *A. grisea* (Chodat) R. K. Jansen (2*x*).—27. *A. serratifolia* R. K. Jansen (2*x*).—28. *A. alpestris* (Griseb.) R. K. Jansen (2*x*).—29. *A. psilocarpa* R. K. Jansen (2*x**).—30. *A. glaberrima* (Hassler) R. K. Jansen (2*x*). Characters.—Taken from Jansen (in press) with the following changes: transformation series 13–15 were eliminated because I felt they were the same as 20–22; transformation series 11 and 12 were combined into one transformation series with two independent apomorphies. Data matrix.—The apomorphies of transformation series 8, 11, and 21 were all treated as independent of one another while in transformation series 2, 17, and 18, apomorphy 1 is of intermediate nature between the plesiomorphic character and the other apomorphy, 2. For Figure 56.

	Apomorphies																	
Taxa	1	2	3	4	5	6	7	8	9	10	11	16	17	18	19	20	21	22
1						1										1		1
2		1	1		1			1								1		1
3a		1	1							1						1	1	1
3b		1	1													1	3	1
4		1	1		1						1					1		
5		1	1						1		1		1			1	3	1
6		1	1								2					1	3	1
7		1	1		1						2		2	2		1	3	1
8		1	1								2			2		1	3	1
9		2	1															1
10		2	1			1										1	2	1
11		2	1			1											2	1
12a		1	1							1								1
12b										1								1
13	1							2			1	1	1	2				1
14	1							2			1		2					1
15a	1							2										1
15b	1																	
15c	1							2										
16a	1									1	2	1		2				1
16b	1									1	2							1
18	1										2			2			3	1
19	1										2		1	2				
20a	1										2		2	2				1
20b	1										1		2	2				
21	1										1		1	1				1
22a				1			1	1		1								1
22b				1		1	1	1							1			1

APPENDIX S. Continued.

	Apomorphies																	
Taxa	1	2	3	4	5	6	7	8	9	10	11	16	17	18	19	20	21	22
22c				1			1				2				1			1
23a		1	1			1	1											1
23b				1		1	1											1
24				1		1	1											1
25				1			1											1
26				1			1											1
27				1			1											1
28				1			1							1	3			1
29				1			1							1	3			1
30				1		1	1	1						1	2			

PHYLOGENETIC ANALYSIS OF SEED PLANTS AND THE ORIGIN OF ANGIOSPERMS[1]

PETER R. CRANE[2]

ABSTRACT

Principles of phylogenetic analysis (cladistics) are introduced with an examination of relationships among extant genera of Gnetales. The Gnetales can be supported as a monophyletic group, with *Gnetum* and *Welwitschia* more closely related to each other than either is to *Ephedra*. Characters of the progymnosperm *Archaeopteris* and 19 extinct and extant seed plant taxa are then reviewed as a basis for a cladistic analysis of their interrelationships. The seed plant taxa included are: medullosans, cycads, *Lyginopteris, Cordaixylon, Mesoxylon, Lebachia,* extant conifers, *Ginkgo, Callistophyton,* peltasperms, glossopterids, *Caytonia,* corystosperms, Bennettitales, *Pentoxylon, Gnetum, Welwitschia, Ephedra,* and angiosperms. Preliminary analyses of relationships within conifers, glossopterids, and Bennettitales are also presented. Results suggest that seed plants are a monophyletic group, and *Lyginopteris* is resolved as the sister taxon to all other seed plants considered. The cordaites, *Cordaixylon* and *Mesoxylon,* along with *Lebachia,* extant conifers, and *Ginkgo* constitute a monophyletic group. *Pentoxylon* is the sister taxon to Bennettitales, and the Gnetales are the sister group to angiosperms. Together the Gnetales plus the angiosperms form the sister group to the Bennettitales plus *Pentoxylon.* If the outer integument of bennettitalean and angiosperm ovules is interpreted as homologous with the "cupule" of *Caytonia* and corystosperms, then the corystosperms are resolved as the sister group to the Bennettitales plus *Pentoxylon* plus Gnetales plus angiosperm clade. Under this interpretation all the seed plant taxa considered except *Lyginopteris,* cycads, and medullosans are part of a single clade in which flattened seeds and saccate pollen are primitive. The principal difficulties with the cladistic analysis concern necessary inferences on unknown characters in certain plants, and the current absence of a large base of comparative data. Results of the analysis suggest that the seed ferns as currently circumscribed are not a meaningful group for phylogenetic purposes and permit an evaluation of the possible phylogenetic position of *Eremopteris, Nystroemia, Spermopteris, Phasmatocycas,* Vojnovskiales, *Leptostrobus,* and several other enigmatic groups of plant fossils. Comparison of the phylogenetic analysis with previous theories of angiosperm origin shows that it reconciles the ideas of Arber and Parkin, that Bennettitales and Gnetales are closely related to flowering plants, with more recent hypotheses that invoke *Caytonia* and corystosperms as highly relevant to the angiosperm problem. The results suggest that increased understanding of Triassic Bennettitales, Gnetales, and corystosperms will be of maximum interest in further elucidating the phylogenetic relationships of flowering plants.

The origin of flowering plants is one of the major unsolved problems of plant phylogeny and an enigma in which most major groups of vascular plants have been implicated. Together with the related question of the origin of the angiosperm flower it has generated a body of literature unrivalled in phylogenetic botany for its size and diversity of opinion. The suggestion that *Magnolia* and related taxa are the most primitive living angiosperms (Arber & Parkin, 1907; Bessey, 1897, 1915) originated at around the turn of the century and reflected a natural extension of the pre-Darwinian systematic tradition of De Candolle and Bentham and Hooker (Davis & Heywood, 1973). The concomitant interpretation of the flower as a reduced bisexual axis bearing ovules and pollen organs on modified leaves (Anthostrobilus or Euanthial theory, Arber & Parkin, 1907) was similarly an extension of the classical idealistic morphology of the nineteenth century. Although the magnoliid theory has never been without its competitors (e.g., Croizat,

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1960; Engler, 1897; Meeuse, 1966; Melville, 1962, 1963; Rendle, 1925, 1930; Sporne, 1971b; Strasburger et al., 1898; Wettstein, 1935), comparative studies of extant flowering plants particularly over the last 20 years (Bailey, 1944; Bailey & Swamy, 1951; Cronquist, 1968, 1981; Dickison, 1975; Eames, 1961; Hickey & Wolfe, 1975; Raven, 1975; Stebbins, 1974; Takhtajan, 1969, 1980; Walker, 1974a, 1974b, 1976; Walker & Doyle, 1975; Wodehouse, 1935, 1936) have reinforced the view that the Magnoliidae sensu lato (Cronquist, 1968, 1981; Takhtajan, 1969, 1980) and perhaps certain monocotyledons (Burger, 1977) are a heterogeneous assemblage of plants that retain a relatively large number of primitive characters for flowering plants as a whole. This conclusion now has been corroborated broadly by the occurrence of the predicted primitive leaf and pollen characters in the earliest angiosperm fossil record (Doyle, 1969, 1973, 1978; Doyle & Hickey, 1976; Hickey & Doyle, 1977; Muller, 1970, 1981, 1984; Sporne, 1974; Upchurch, 1984; Walker & Walker, 1984; Wolfe et al., 1975). The sequential stratigraphic appearance of progressively more complex leaves and pollen (Brenner, 1963; Doyle, 1969; Doyle & Hickey, 1976; Hickey & Doyle, 1977; Hughes, 1976; Muller, 1970, 1984) has been interpreted as documenting a major mid-Cretaceous flowering plant radiation beginning in the Barremian or earlier in the Lower Cretaceous (Brenner, 1984; Trevisan, pers. comm.). Palynological evidence suggests that this radiation began at low, tropical, paleolatitudes and was followed by predominantly poleward migration (Brenner, 1976; Hickey & Doyle, 1977). Reports of pre-Cretaceous angiosperms either have been rejected or must be regarded as of uncertain relevance due to lack of critical information (Doyle, 1978; Hill & Crane, 1982; Scott et al., 1960). Reconstructions of some early angiosperms from several dispersed organs (Dilcher & Crane, 1984) and studies of flowers and other reproductive structures (Basinger & Dilcher, 1984; Crane & Dilcher, 1984; Dilcher, 1979; Krassilov et al., 1983; Vakhrameev & Krassilov, 1979) also have provided important insights into the systematic relationships, floral morphology, and reproductive biology of some early flowering plants.

Despite this success in clarifying the timing and pattern of the early flowering plant radiation, the fundamental question of the phylogenetic position of angiosperms in the overall scheme of seed plant evolution remains unanswered. Some have claimed that we are no closer to a consensus as to which group of gymnosperms might be most relevant than we were at around the turn of the century (Beck, 1976; Harris, 1960; Hughes, 1976). Discussions of this problem have generally centered on two interrelated issues: the origin of the angiosperm carpel, and the ancestors of flowering plants.

There have been many hypotheses as to the derivation of the angiosperm carpel from the ovulate reproductive structures of living and fossil gymnosperms. The most common proposition derives the conduplicate carpel from the ovulate structures of pteridosperms (seed ferns) sensu lato: either *Caytonia* (Andrews, 1963; Doyle, 1978), corystosperms (Stebbins, 1974), *Glossopteris* (Retallack & Dilcher, 1981), or even Carboniferous seed ferns (Long, 1966, 1977). Although none of these hypotheses has received universal acceptance, they have contributed to a widespread view that the outer integument of the normally bitegmic angiosperm ovule is homologous to the cupule of seed ferns (Smith, 1964), and that the pteridosperms are the ancestors of flowering plants (Cronquist, 1968, 1981; Knoll & Rothwell, 1981; Stewart, 1983).

Much of the literature reviewed above implies that solution of the angiosperm problem must necessarily involve the recognition of angiosperm ancestors (e.g., Mabberley, 1984). This is a position confronted by theoretical and practical difficulties. First, if our current understanding of evolutionary processes is accurate, then it is species, not higher taxa, that are the units of evolution, and thus only species and not higher taxa can be truly ancestral (Eldredge & Cracraft, 1980: 114); and second, ancestral groups cannot be defined by features that they alone possess, because by definition these features also characterize members of the descendant group (Wiley, 1979: 212–214). Under such circumstances it is inevitable that many ancestral groups have been construed loosely and used broadly to indicate inferred proximity of descent. A system in which groups are not clearly defined, and similarity is hazily interpreted as phylogenetic relationship, may have heuristic value, but inevitably it is only capable of generating broad, relatively unspecific conclusions that are difficult to compare. It does not facilitate explicit, and thus critical, evaluation of alternative suggestions of relationship (Hill & Crane, 1982).

Phylogenetic systematics (Hennig, 1966; often treated as synonymous with cladistics) offers an

alternative approach to the question of angiosperm origins. It can provide a relatively explicit assessment of relationships from which straightforward evolutionary interpretations can be made and a methodological framework in which competing theories of relationship may be compared usefully. It also provides an alternative to the search for ancestral groups, allowing phylogenetic problems to be formulated in a different and more tractable fashion. In cladistic terms the problem of angiosperm origin is to recognize and define the major groups of seed plants, to determine their phylogenetic interrelationships, and thus to establish with which group of gymnosperms the flowering plants share a most recent common ancestor (Crane, 1984).

The large-scale phylogenetic relationships of seed plants have been the subject of very little critical discussion, and there is little agreement on how the major taxa should be grouped together. Many recent classifications have either adopted or modified the views of Coulter and Chamberlain (Chamberlain, 1935; Coulter & Chamberlain, 1917) formulated over half a century ago (Bierhorst, 1971; Cronquist et al., 1966; Foster & Gifford, 1974; Sporne, 1971a). Other authors have merely treated all the major groups as of equivalent rank (Bold, 1973; Bremer & Wanntorp, 1981; Taylor, 1981a). The late Professor Tom Harris succinctly summarized the situation when he commented (1976: 133) that the "classes" of gymnosperms were no longer the "branches of a single phylogenetic tree," but "a dozen separate trees rooted in the unknown." This paper attempts to systematize available data on fossil and living seed plants, to clarify their relationships, and establish a coherent framework within which the position of flowering plants may be assessed.

There have been two previous attempts to evaluate relationships within seed plants using cladistic techniques. Both were preliminary and intended in part to stimulate future work. Parenti (1980) produced a highly resolved arrangement of seven major groups, but her analysis was criticized by Smoot et al. (1981) and Young and Richardson (1982) (see also reply by Parenti, 1982). The principal difficulties with her analysis concerned the heterogeneity, and hence monophyly, of some taxa, and the level of detail of character definition. Hill and Crane (1982) presented an analysis based solely on extant seed plants using living *Equisetum*, lycopods, and ferns as out-groups. Our analysis also encountered difficulties with character definition and recognition. Fifty characters were surveyed but yielded several alternative solutions that, although dramatically different, were almost equally parsimonious. This paper extends and attempts to improve on the analysis by Hill and myself. It reanalyzes and redefines many of the characters employed, includes additional characters, and incorporates for the first time some of the better understood fossil gymnosperms. In the absence of detailed cladistic analyses of the larger gymnosperm groups (e.g., conifers), outline cladograms are proposed as a basis for recognizing advanced and primitive characters in those taxa.

The paper is divided into four major parts. First, the principles of cladistics are introduced briefly and illustrated by a simple analysis of relationships between the three extant genera of Gnetales. Second, the characters of extant, and sufficiently well known fossil, seed plants are reviewed and phylogenetic relationships are assessed. Third, an overview of seed plant phylogeny is presented and compared with previous classifications and phylogenetic hypotheses. Finally, the possible phylogenetic relationships of other more poorly understood plant fossils are reviewed and problems for future research are discussed. Throughout, it should be noted that higher taxa are referred to as far as possible by informal names that have no implication of taxonomic rank. The primary concern is to clarify relationships, and I make no suggestions as to how these should be summarized as a formal nomenclatural scheme. Fossil taxa are treated as "whole plants." Justification for individual cases is given in the text. In the descriptive sections the megasporangiate reproductive structures are referred to as "ovules" except where embryos are known to be present. The terms megasporophyll and microsporophyll are used throughout for simplicity of comparison, but it is by no means clear in many gymnosperms whether the reproductive structures are leaf or shoot homologues. Individual cases are discussed in the text. The numbers assigned to characters are prefixed by the number of the table in which they are listed.

PHYLOGENETIC RELATIONSHIPS IN THE GNETALES—A THREE-TAXON PROBLEM

PRINCIPLES

In a cladistic analysis each of the taxa under consideration should be a monophyletic group.

As far as I know no one has seriously questioned the naturalness and, by implication, the monophyly of any of the three extant gnetalean genera. *Welwitschia* is in any case monotypic. It is a bizarre xerophyte occurring only in restricted desert areas of southwest Africa (Chamberlain, 1935). *Gnetum* comprises about 40 species of predominantly tropical lianes but also includes a few trees and shrubs (Sporne, 1971a). *Ephedra* comprises about 40 species of "switch" shrubs with less common tree-like and vine-like forms (Sporne, 1971a). The genus occurs in xeric habitats at low, but generally extra-tropical, latitudes.

Not all of the characters of these genera can contribute to resolving relationships within the Gnetales. Features restricted to a single genus may account for its distinctiveness but are clearly of no value for interpreting relationships with other genera. Similarly, features that occur in all three genera may be useful for defining the limits of the Gnetales as a group but cannot contribute to defining inter-generic relationships. Characters that occur in two of the three extant genera may provide an indication of relationship but are of two kinds: those that could define an exclusive group of two gnetalean genera in which no other taxon would be included, and less restricted characters that could only define a group in which non-gnetalean taxa would also have to be included. Characters of the first kind suggest that two gnetalean genera are more closely related to each other than they are to any other taxon, while characters of the second kind merely indicate that the two genera are no more closely related to each other than either is to some non-gnetalean plant. Characters of the second kind are of no value for assessing phylogenetic relationships among the three gnetalean genera, and cladistics attempts to recognize and utilize only characters of the first kind. This is accomplished by assessing the distribution of characters in related groups ("out-group comparison," Hill & Crane, 1982: 280; Stevens, 1980, 1981; Watrous & Wheeler, 1981). Theoretically the out-group for the Gnetales could be all other organisms, but for practical purposes a more manageable out-group could be all other seed plants or all other vascular plants. In this example all seed plants, with the exception of flowering plants, are used as the out-group. The effect of incorporating flowering plants is considered later in this paper.

To assess whether the tetrasporic megagametophyte of *Welwitschia* and *Gnetum* defines an exclusive group, and therefore suggests close relationship, the distribution of the tetrasporic and monosporic condition is examined in all seed plants. All other seed plants (excluding some angiosperms) are monosporic. The tetrasporic condition is relatively restricted and defines an exclusive group (*Welwitschia* plus *Gnetum*). Conversely, the cellular female gametophyte seen at fertilization in *Welwitschia* and *Ephedra* is merely an expression of the condition that occurs in all other seed plants except *Gnetum* and angiosperms. In *Gnetum* the female gametophyte is partially free nuclear at the time of fertilization. The character is therefore of no value for assessing relationships between the gnetalean genera.

Assessing the generality (polarity) of characters by out-group comparison inevitably involves a logical regress in that decisions can be made only by reference to groups already circumscribed (perhaps wrongly) by the distribution of yet other characters (Hill & Crane, 1982: 280). However, the process can be used to develop a hypothesis about which of a pair of contrasted characters is more, or less, restricted. This is open to test by broadening the analysis still further. When applied to a variety of characters these assessments of generality result in a character hierarchy that defines groups within groups, for example, a multicellular embryo developing within an archegonium (embryophytes), vascular tissue of tracheids and/or vessels (tracheophytes), seeds (seed plants, spermatophytes), or a megaprothallus of four to 16 nuclei (angiosperms) (Fig. 1). In this way relationships can be defined in relative terms (Hennig, 1965: 98). *Ginkgo* and *Pinus* both have seeds (spermatophytes) and are therefore more closely related to each other than either is to *Lycopodium* (a pteridophyte), which is free sporing and lacks seeds.

All characters may be useful for defining groups at some level in the hierarchy (Wiley, 1981: 126), but at any given level of inclusiveness (universality) some characters will be useful for group definition, whereas others will not. The implementation of this distinction is the fundamental difference between cladistics and phenetics. At any level in the hierarchy the phenetic concept of "overall similarity" is separated into a generalized, cladistically non-definitional component (symplesiomorphy), and a less generalized, definitional component (synapomorphy).

In practice recognizing apparent synapomor-

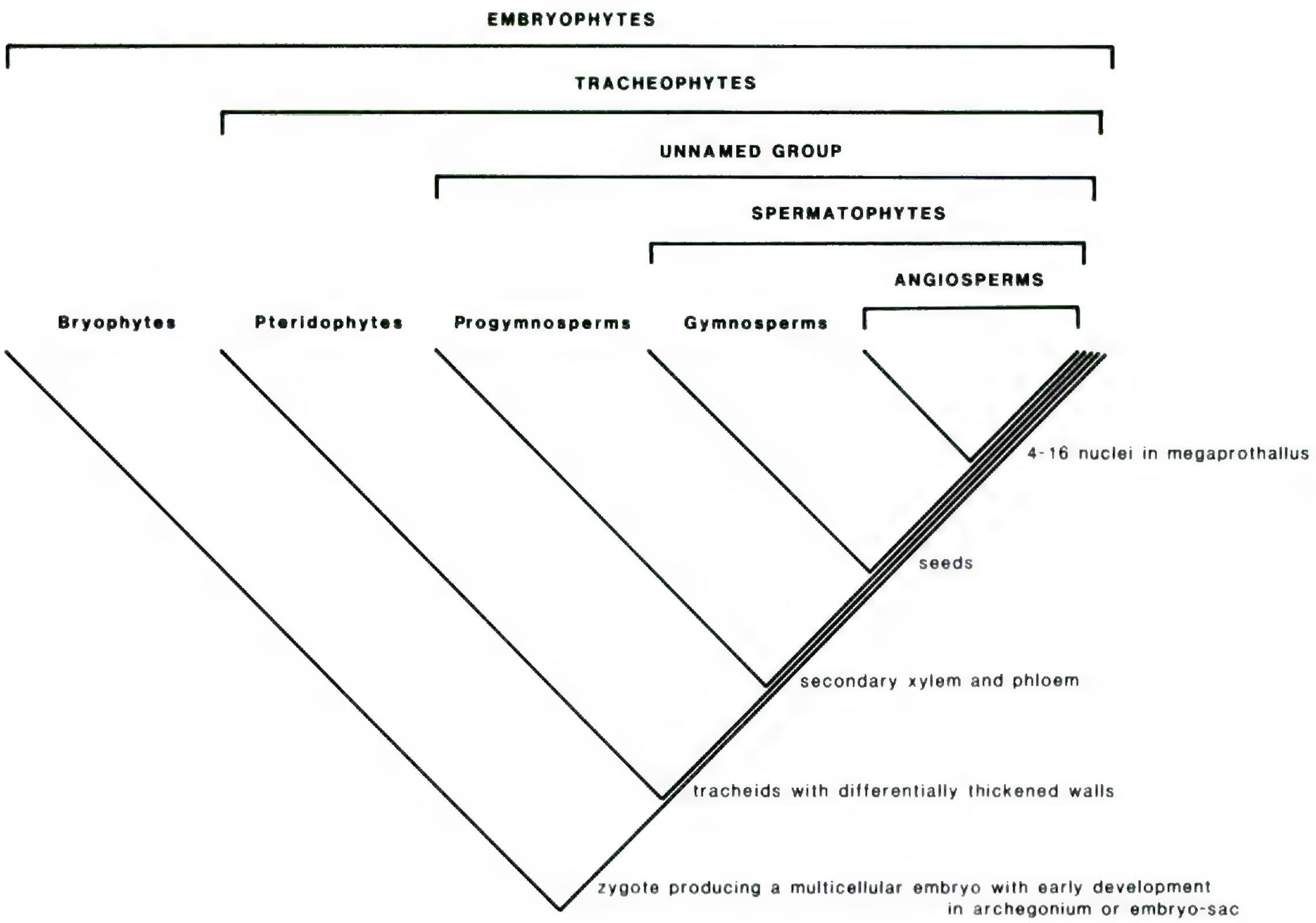


FIGURE 1. A simplified summary of character distributions in embryophytes and the subclasses that they define. Groups definable by presence of a single character given in upper case. Such groups may be regarded as monophyletic. Widely used grade groups only definable by combined presence and absence of characters shown in this diagram are given in lower case. Unless these groups can be shown to have unique defining characters, they are regarded as paraphyletic. For further details of relationships within the bryophyte grade see Mishler and Churchill (1984).

phies and identifying their distribution seldom produces a single unambiguous character hierarchy. Different characters often indicate conflicting groups and hierarchical patterns. Applying the principle of parsimony, it is the simplest of competing patterns that is preferred. In effect, parsimony minimizes the conflict between apparent synapomorphies and therefore the conflict between apparent groups (Farris, 1982; Wiley, 1981). In cladistic terms the "true synapomorphies" recognized in this way are homologies, and the problems of determining polarity, synapomorphy, and homology can therefore be viewed as synonymous (Eldredge & Cracraft, 1980: 35–40; Hill & Crane, 1982: 282–287; Patterson, 1982a; Stevens, 1984). The result of a cladistic analysis is therefore merely a pattern of nested synapomorphies. It defines relationships in a relative way and like any other hierarchical pattern may be summarized in a tree-like diagram. There is no necessary relation to the theory of evolution and no necessary time axis.

Although such diagrams can thus be largely independent of evolutionary preconceptions (Nelson, 1979; Patterson, 1982b; Platnick, 1979, 1982), most systematists wish to interpret them in phylogenetic terms (Crane & Hill, in press; Hill & Crane, 1982; Wiley, 1981). Indeed, for many systematists, the compatibility between cladistic reasoning and current concepts of character change during phylogeny is an important reason for preferring a cladistic rather than a phenetic approach. Interpreted in terms of phylogeny the nested synapomorphies can be viewed as a nested sequence of homologous evolutionary novelties, and the problem of determining character polarity as a problem of deciding which characters represent modifications of which—in other words, which characters are relatively derived or advanced. Groups defined by synapomorphies (clades) can be interpreted as including a common ancestor and all its descendants (monophyletic). Groups such as the gymnosperms and pteridophytes (Fig. 1) that contain

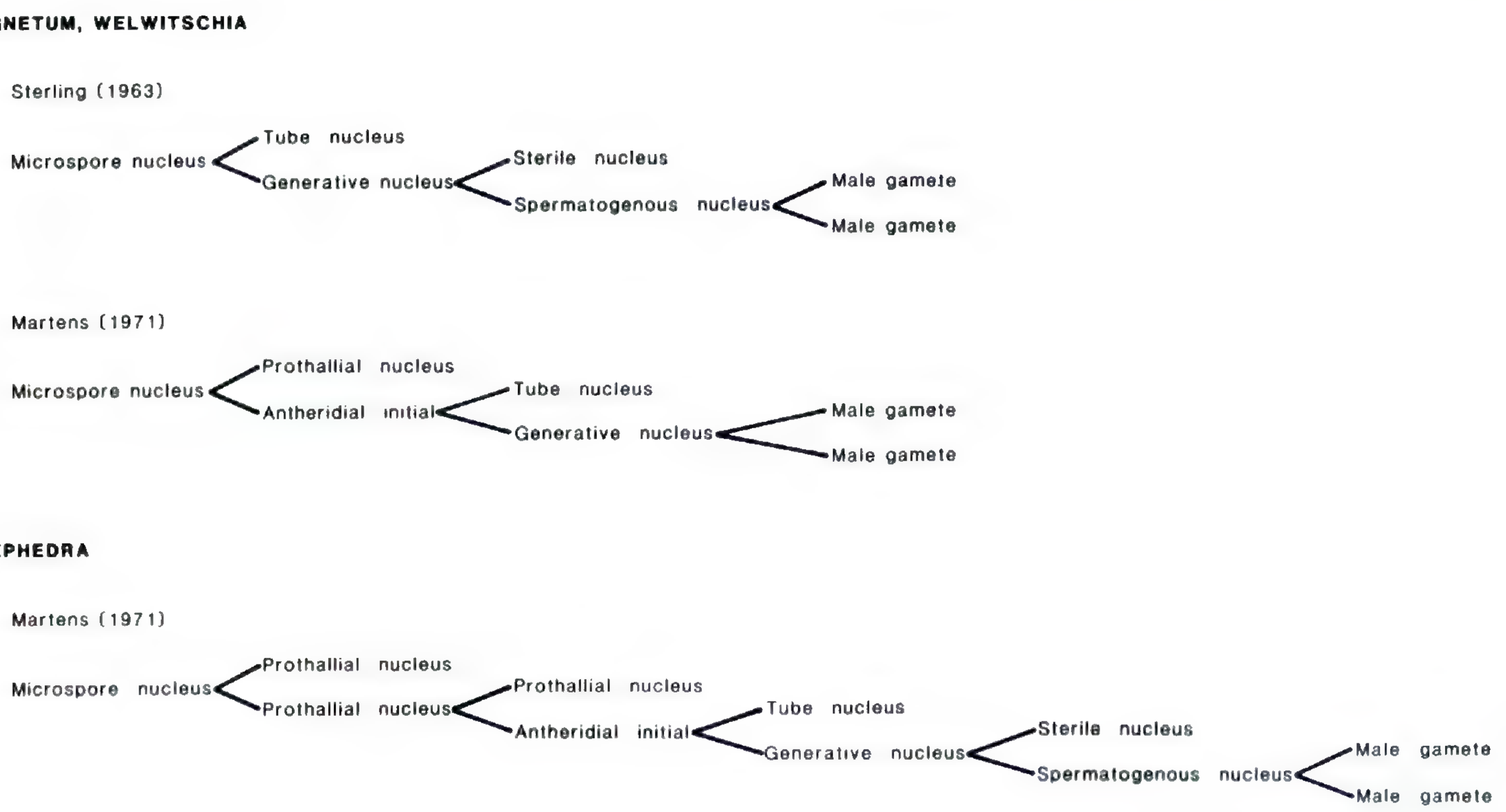


FIGURE 2. Comparison of male gametophyte development in *Gnetum, Welwitschia,* and *Ephedra.* See text for further explanation.

some, but not all, of the descendants of a common ancestor (paraphyletic), may be interpreted as definable only by a combination of shared primitive and advanced features. The vertical axis of the cladogram can be interpreted as relative time and the nodes as hypothetical ancestors. Relationships may be viewed in terms of relative recency of common ancestry (Bigelow, 1956; Hennig, 1966). *Ginkgo* shares a more recent common ancestor with *Pinus* than either does with *Lycopodium.* Finally, the principle of parsimony can be viewed as a criterion for selecting between competing cladograms in which homoplasy (parallelism, convergence, and reversal) is minimized.

ANALYSIS OF CHARACTERS

1.1 Male gametophyte composed of four nuclei. In *Gnetum* and *Welwitschia* three haploid mitoses produce a male gametophyte of four nuclei (Martens, 1971; Sterling, 1963), though the pollen may be dispersed at the bi-nucleate or tri-nucleate stage. According to Martens (1971: 146, 260), the gametophyte consists of a prothallial nucleus, a tube nucleus, and a generative nucleus, which produces two male gametes directly without division into sterile and spermatogenous nuclei. Sterling (1963: 195) interpreted the prothallial nucleus of Martens as a "tube nucleus" and the tube nucleus as a "sterile nucleus" (Fig. 2; see Sterling, 1963, for a more detailed consideration of terminology). In *Ephedra,* the microspore undergoes five haploid mitoses to produce a six-celled microgametophyte consisting of two prothallial nuclei, a tube nucleus, a sterile nucleus (stalk nucleus), and a spermatogenous nucleus (body nucleus) (Martens, 1971: 48, 260). The pollen is dispersed with five free nuclei.

The development of the male gametophyte in *Ephedra* is similar to that in Araucariaceae, Pinaceae, and Podocarpaceae (Sterling, 1963). In *Ginkgo* there is also a six-celled microgametophyte, but the details of development (particularly of the motile gametes) differ from those of *Ephedra* and conifers (Lee, 1955). Within the conifers, Cephalotaxaceae, Taxaceae, Taxodiaceae, and most Cupressaceae apparently have only three haploid mitoses and lack prothallial cells (Sterling, 1963), as in *Gnetum* and *Welwitschia.* In most cycads, there are four mitotic divisions, and only one prothallial cell is produced (Sterling, 1963). By out-group comparison with pteridophytes I interpret the more extensive five- and six-celled male gametophyte as the more generalized condition and regard the four-celled condition as relatively specialized. Because the conifers are accepted as a monophyletic group in this paper (p. 727), reduction of the male gametophyte must have occurred at least twice in seed plants, once within the conifers, and once within the Gnetales. The character can never-

theless be regarded as a potential synapomorphy in the Gnetales that unites *Gnetum* and *Welwitschia.*

1.2 Female gametophyte tetrasporic. In *Gnetum* and *Welwitschia,* the female gametophyte is tetrasporic, being the meiotic product of a single megaspore mother-cell without the formation of cell walls (Martens, 1971: 261). In *Ephedra,* which is monosporic, the megaspore mother-cell produces a linear tetrad of megaspores, the lowermost of which enlarges and divides to form the female gametophyte. Occasionally wall formation between the megaspores may be slightly delayed (Lehmann-Baerts, 1967). The monosporic condition occurs in conifers, *Ginkgo,* cycads, and most angiosperms, and the tetrasporic condition therefore is interpreted on out-group comparison as a derived character.

1.3 Archegonia absent. In *Gnetum* and *Welwitschia,* no archegonia differentiate in the female gametophyte (Martens, 1971; Sporne, 1971a). In *Gnetum* this reflects the free nuclear condition of the micropylar end of the gametophyte at fertilization, whereas the female gametophyte of *Welwitschia* is cellular at fertilization, and although archegonial initials can be detected, they do not develop (Singh, 1978). In *Ephedra,* two or three archegonia differentiate from the superficial cells of the gametophyte and consist of an egg cell, a ventral canal cell, and a distinct neck (Martens, 1971, figs. 30, 31). In conifers, *Ginkgo,* and cycads, the archegonia are well differentiated (Sporne, 1971a: 115, 137, 169). From out-group comparison I interpret the absence of archegonia in *Gnetum* and *Welwitschia* as a derived character.

1.4 Embryo with "feeder." The mature embryo in *Gnetum* and *Welwitschia* has a lateral, finger-like extension of the hypocotyl, termed a "feeder" (Sporne, 1971a: 179). It remains embedded in the seed after germination and may have an absorptive function. In *Gnetum* the "feeder" is massive and vascularized but is generally less well developed in *Welwitschia* (Martens, 1971: 251). No comparable structure occurs in *Ephedra* or other gymnosperms (Sporne, 1971a: 179), suggesting that it is a specialized feature of *Gnetum* and *Welwitschia.*

1.5 Ribbed pollen. Pollen of *Gnetum* is spheroidal, generally 20 μm or less in diameter, with small spinules. The grains are typically inaperturate, but some have a single, thin and poorly defined pore-like area (leptoma) (Erdtman, 1957, 1965: 42–44). Pollen of *Welwitschia* is ellipsoidal, approximately 50 μm long, and the exine has about 20 longitudinal ribs separated by shallow grooves. One of the grooves is larger and forms a poorly defined, elongated aperture (Erdtman, 1957, fig. 30, 1965: 80–81; Wodehouse, 1935, 1936). Pollen of *Ephedra* is similar to that of *Welwitschia.* Grains are ellipsoidal, approximately 20–40 μm long, with 15–18 straight or zig-zag longitudinal ribs separated by grooves that are V-shaped in section. There is no apertural region like that in *Welwitschia* (Erdtman, 1957, fig. 30, 1965: 37–41; Steeves & Barghoorn, 1959; Wodehouse, 1935, 1936). The pollen of living conifers, *Ginkgo,* and cycads shows no close similarities with that of any gnetalean genus; however, the ribbed pollen in *Welwitschia* and *Ephedra* is unique and interpreted here as specialized within seed plants.

1.6 Vessels. Vessel elements occur in all three genera of Gnetales. The early protoxylem tracheids are unusual and have circular bordered pits associated with annular or helical wall thickenings (Bierhorst, 1960: 281). These are modified to form pores only in the elements differentiated later in ontogeny (Bierhorst, 1960). In *Gnetum* the later protoxylem tracheids have pores towards their ends. These appear to develop from large pits by loss of pit membranes and frequently by a reduction in the width of the pit border (Bierhorst, 1960: 280–283; Bliss, 1921). Generally there are fewer than six widely spaced pores arranged in a uniseriate row (Bierhorst, 1971: 473). The metaxylem tracheids generally contain fewer pores, and they are arranged in contact with each other. In the secondary xylem, the perforation plates are often transversely oriented and may consist of groups of pores or a single pore (Bierhorst, 1971: 473; Thompson, 1918). These simple plates represent at least two different situations: true simple pores, and compound structures formed by loss of the secondary wall between several adjacent pores (Bierhorst, 1971: 473). Muhammad and Sattler (1982) document the extreme variability in the perforation plates of *Gnetum* and discuss their mode of formation.

In *Welwitschia* the pores in the protoxylem are generally single, and a row of two or three is rare. In the metaxylem and secondary xylem only single pores occur, and there is no evidence that they arise by fusion of several smaller ones as in *Gnetum* (Bierhorst, 1960: 287).

In *Ephedra* the late protoxylem and early metaxylem vessel members typically have more pores than those of *Gnetum.* They are arranged

in a uniseriate row, but in the late metaxylem and secondary xylem the pores tend to be arranged in compact groups. Simple perforation plates are very uncommon (Bierhorst, 1960: 281).

Vessels do not occur in any other gymnosperm and are clearly relatively specialized within seed plants. They are, however, present in some, presumably only distantly related, pteridophytes (Bierhorst, 1958, 1960, 1971). On this basis they are accepted here as a potential synapomorphy of the Gnetales (see p. 767 for discussion of vessels in flowering plants).

1.7 Microsporangiate and ovulate "flowers" with opposite pairs of bracteoles. The microsporangiate and ovulate "flowers" of the Gnetales are arranged on a fundamentally similar plan that provides a unifying character for the group. Each "flower" is comprised of a system of opposite and decussate bracteoles axillary to a primary bract (Martens, 1971: 256). Interpretations of the homologies of the bracts, bracteoles, and various envelopes that they form have varied, and an enormous literature has accumulated (Martens, 1971; Pearson, 1929). The explanation of homologies given here is based on a straightforward interpretation of the currently available data.

In *Gnetum* the inflorescences may be "unisexual" or "bisexual," but both are elongated and have whorls of reproductive structures. Microsporangiate and ovulate "flowers" are aggregated into one or more whorls subtended by a fleshy ring-like collar ("cupule" of Pearson, 1929). The base of the inflorescence is subtended by a pair of opposite bracts (Martens, 1971, figs. 102.1, 105.1, 107; Pearson, 1929, fig. 35). The lowermost collar frequently has two teeth oriented at 90° to the two basal bracts, and, if several collars with teeth are present, their arrangement is opposite and decussate (Martens, 1971; Pearson, 1929: 56). Although most collars do not have teeth and show no evidence of bipartite structure in their ontogeny (Martens, 1971: 208–209), they generally are interpreted to have arisen by the phylogenetic fusion of two opposite bracts (Pearson, 1929: 56). In ovulate spikes there are usually one or two rings of fertile ovulate "flowers" (Pearson, 1929: 57–58) above each other. In microsporangiate spikes there are frequently several whorls of "flowers," the upper of which in some species (e.g., *G. gnemon,* Pearson, 1929: 57) are ovulate but "incomplete" (see below) and nonfunctional. "Floral" primordia develop adaxially from an annular meristem at the base of the supraadjacent developing collar (Martens, 1971, fig. 102.4), but the axillary position of the "flowers" is clearly demonstrated by their vasculature. The arrangement of "floral" vascular bundles may be complex, but the traces are predominantly derived from the bundles that supply the collars (Pearson, 1929: 62–68; Thoday, 1911).

The microsporangiate structures of *Gnetum* are surrounded at the base by a tubular "perianth" that has two median lobes at the apex (Martens, 1971: 257; but see Pearson, 1929). There is some indication of bipartite structure during early ontogeny (Martens, 1971: 213, fig. 110.5, 110.6), and the perianth is generally interpreted as having been phylogenetically derived from two posterior-anterior bracteoles (Fig. 3A; Bierhorst, 1971: 475; Sporne, 1971a).

The nucellus in *Gnetum* is surrounded by three envelopes (Fig. 3B) that have been variously interpreted (Martens, 1971; Pearson, 1929). All three layers arise ontogenetically as circular meristems, the outer differentiating first (Martens, 1971, fig. 104). The inner layer, interpreted here as the only integument, is extended at the apex into an elongated micropylar tube that extends beyond the two outer envelopes. The middle and outer layers give no indication of an origin from pairs of opposite bracteoles (Martens, 1971), and that interpretation (Fig. 3C) hinges solely on reconciling the structure of *Gnetum* with that of *Ephedra* and *Welwitschia* (see below). In "incomplete" flowers of *Gnetum* the middle layer begins to develop but then aborts (Chamberlain, 1935: 416).

In *Welwitschia* the microsporangiate and ovulate inflorescences are dichasially branched (Sporne, 1971a: 180), and the ultimate branches terminate in cones with opposite and decussate bracts ("cone-scales," Sporne, 1971a: 180). The microsporangiate "flowers" (Fig. 3D) are the most complex "floral" structures in the Gnetales. Each consists of a central sterile ovule with a single integument and elongated micropylar tube expanded at the apex into a papillose funnel-shaped opening (Martens, 1971: 134–135; Sporne, 1971a). At the base of the ovule there are two small lateral flaps (Martens, 1971, fig. 71.11). The ovule is surrounded by a cup-like structure bearing two lateral, two dorsal, and two ventral microsporangial stalks. Each stalk has a terminal trilocular sporangium that dehisces by three radial slits at the apex. In addition to the two lateral sporangia there are also two lateral "pseudostaminal" primordia (Martens, 1971: 137–142).

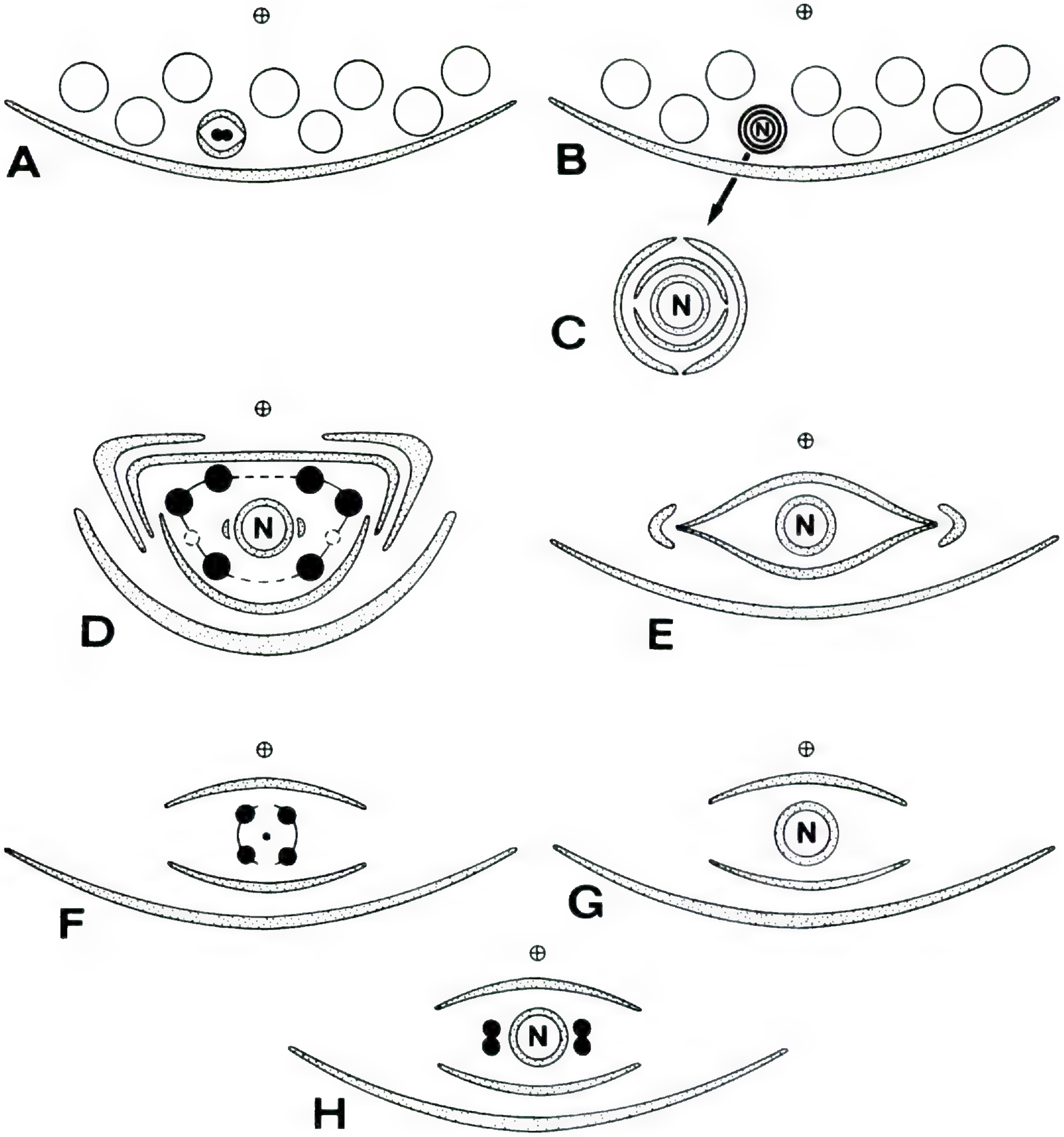


FIGURE 3. Comparison of microsporangiate and ovulate "floral" diagrams in the Gnetales.—A. *Gnetum* microsporangiate "flower," after Martens (1971, figs. 105.4, 105.7, 110.5, 110.6).—B. *Gnetum* ovulate "flower," after Martens (1971, figs. 103, 104).—C. *Gnetum* ovulate "flower," interpretation, see text (character 1.7) for explanation.—D. *Welwitschia* microsporangiate "flower," redrawn from Martens (1971, fig. 70.6).—E. *Welwitschia* ovulate "flower," redrawn from Martens (1971, fig. 63.6).—F. *Ephedra* microsporangiate "flower," after Eames (1952, fig. 1A).—G. *Ephedra* ovulate "flower," based on Martens (1971).—H. *Ephedra* abnormal microsporangiate "flower," after Mehra (1950: 176, pl. V.2). N = nucellus.

Outside the microsporangiate cup there is an inner anterior-posterior pair of bracteoles oriented parallel to the primary bract and an outer pair of lateral bracteoles.

The ovulate "flowers" of *Welwitschia* (Fig. 3E) are organized on a plan very similar to those with microsporangia. The single ovule has an elongated micropylar tube but it is not expanded at the apex. There are no microsporangiate structures, or any indication of them, but there is an inner pair of anterior-posterior bracteoles (that form the wing in "fruit") and an outer pair of lateral bracteoles.

The microsporangiate and ovulate inflorescences of *Ephedra* are borne in axillary position and vary considerably in their degree of branch-

ing (Pearson, 1929). The "flowers" are clustered into "cones" with an opposite and decussate arrangement of primary bracts. The microsporangiate "flowers" (Fig. 3F) consist of a two-lipped "perianth" that arises from two anterior-posterior primordia (Pearson, 1929: 76) and surrounds the base of the microsporangiate structures. The morphology of the microsporangiate structures varies among species. In *E. distachya, E. intermedia,* and *E. trifurca* there are two or more separate sporangiophores, sometimes with a protruding, vascularized axial remnant between them (Bierhorst, 1971: 467; Chamberlain, 1935: 369; Eames, 1952). Eames (1952) interprets this condition as primitive. In other species, such as *E. antisyphilitica* (Bierhorst, 1971: 467), the sporangiophores form a compound columnar tube. Eames (1952) regards this condition as relatively advanced. The number of sporangia varies from two to eight, forming a trilocular, quadrilocular, or more typically bilocular synangium at the apex of the columnar tube (Pearson, 1929: 75).

The ovulate "flowers" of *Ephedra* (Fig. 3G) are organized similarly to those with microsporangia. Generally only the uppermost pair of primary bracts in a "cone" is fertile (Pearson, 1929: 54–55), and the lower bracts frequently become red and fleshy at maturity: presumably they aid in dispersal. Each bract subtends one "flower." The ovule has a single integument with an elongated micropylar tube that exhibits a range of morphologies in different species (Pearson, 1929: 79). The "perianth" has been variously interpreted (Martens, 1971: 41), but consists of two anterior-posterior bracteoles that may be free or connate at their margins (Eames, 1952: 88). These form the "husk" of the "fruit" at maturity.

There is a direct correspondence between the structure of microsporangiate and ovulate "flowers" in *Ephedra,* and the "perianth" of both appears homologous (Eames, 1952). This is supported further by the similarity of poorly developed "perianths" in ovulate "flowers" to the normal "perianth" in microsporangiate "flowers" (Mehra, 1950: 177–178). There is also a close similarity between the microsporangiate "flowers" of *Ephedra* and *Gnetum* (Pearson, 1929: 75), and the microsporangia in both are supplied by two vascular strands (Mehra, 1950). The arrangement of bracts and bracteoles in these three "flowers" differs from the organization in *Welwitschia* only in the absence of the outer lateral bracteoles from the microsporangiate and ovulate "flowers." I suggest that the "perianth" in *Ephedra* and *Gnetum* is homologous with the inner bracteoles of *Welwitschia,* and that merely the lateral outer bracteoles are missing. This suggestion is supported by the fact that the microsporangia in *Ephedra* are in fact arranged in a whorl like those of *Welwitschia,* and that where bisporangiate "flowers" of *Ephedra* have been reported (Mehra, 1950: 168–169) the microsporangia occur where expected (Fig. 3H): surrounding the ovule but inside the "perianth" (Mehra, 1950: 177). Only the two outer envelopes around the ovules in *Gnetum* remain unaccounted for. These show no sign of having fused, either phylogenetically or ontogenetically (but see Martens, 1971: 203), from pairs of bracteoles. However, their position, and the occurrence of microsporangia between the integument and the middle layer (inner bracteoles) in abnormal flowers of *G. scandens* (Thompson, 1916), suggest a direct equivalence with the inner and outer bracteoles of *Welwitschia* (compare Fig. 3C, E). Certainly they cannot be reconciled more easily with the reproductive structures of any other gymnosperm. These views on the homology of gnetalean flowers are summarized in Figure 3; their organization is unique within seed plants. On this basis they are interpreted here as a potential synapomorphy of the Gnetales.

DISCUSSION AND INTERPRETATION

The data matrix for the seven characters of the Gnetales is given in Table 1 and the resulting cladogram in Figure 4. The results suggest that the Gnetales are a monophyletic group (see also Arber & Parkin, 1908; Hill & Crane, 1982) within which *Gnetum* and *Welwitschia* are more closely related to each other than either is to *Ephedra.* The Gnetales are separated from all other gymnosperms and united as a group by their fundamentally similar floral organization (character 1.7) and the presence of vessels (character 1.6). Their monophyly is further supported by the occurrence of opposite and decussate leaves in all genera (but not all species, Bierhorst, 1971; Foster & Gifford, 1974; Gifford & Corson, 1971; Sporne, 1971a) and the presence of a stem apex with a discrete tunica (Foster & Gifford, 1974; Martens & Waterkeyn, 1963, Voronin et al., 1973) unlike the typical condition in gymnosperms (Gifford & Corson, 1971; Johnson, 1951; Sporne, 1971a: 110, 133, 167, 184). This agrees with the view expressed by Bierhorst (1971) and Coulter

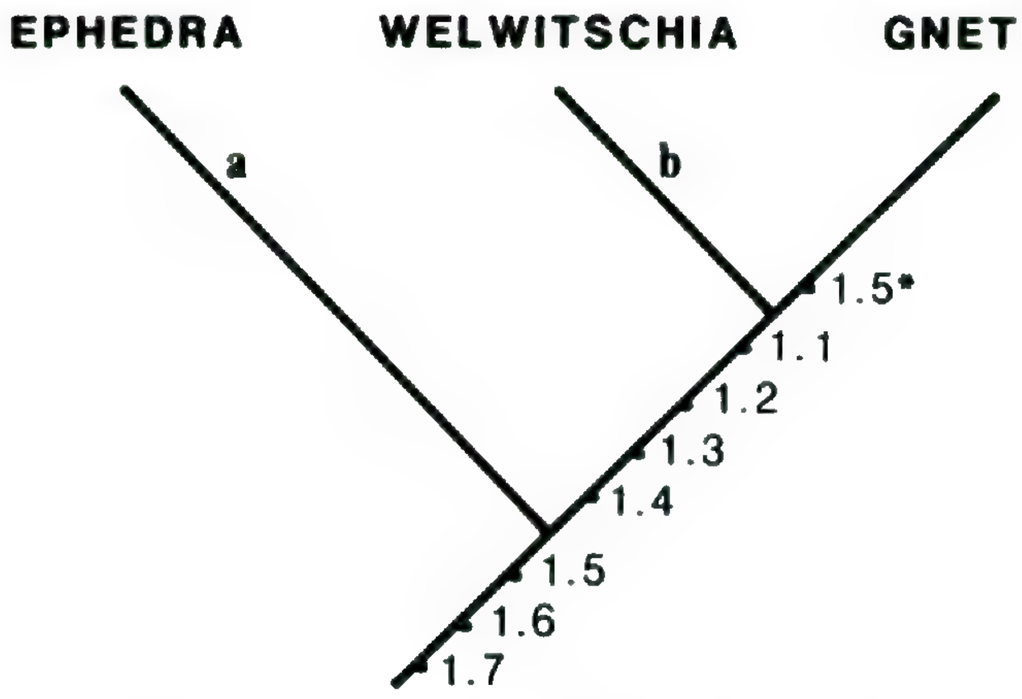


FIGURE 4. Cladogram summarizing relationships between *Gnetum, Welwitschia,* and *Ephedra* based on the data in Table 1. See text for further explanation. Viewed methodologically character 1.5 could be interpreted as having been derived independently in *Ephedra* and *Welwitschia* (a, b) or as having been secondarily modified in *Gnetum* (1.5*). From an evolutionary perspective ribbed pollen is more likely to be primitive within the Gnetales and to have been subsequently modified in *Gnetum.*

and Chamberlain (1917: 402) that, "whatever may be the connections of *Ephedra* with other gymnosperms . . . it cannot be separated from *Welwitschia* and *Gnetum.*"

Additional evidence for a close phylogenetic relationship of *Gnetum* and *Welwitschia* is provided by: the presence of asterosclereids (Bierhorst, 1971: 475; "spicular cells," Martens, 1971: 255), the occurrence of vestured pits in the early protoxylem (Bierhorst, 1960), the occurrence of paracytic (but not exclusively syndetocheilic) stomata (Florin, 1951, fig. 7e; Maheshwari & Vasil, 1961; Martens, 1971, fig. 96I), totally cellular embryogenesis (Martens, 1971: 765), and the irregular cellularization that occurs during female gametophyte development resulting in multinucleate cells and the formation of fusion nuclei (Martens, 1971: 262). *Ephedra* is cladistically more primitive. Eames (1952) has emphasized how "distantly related" *Ephedra* is from *Welwitschia* and *Gnetum,* and Coulter and Chamberlain (1917: 403) concluded that, "*Welwitschia* and *Gnetum* are farther removed from other gymnosperms than is *Ephedra.*" Some of the similarities that *Ephedra* shares with conifers have been mentioned above, and in cladistic terms these are interpreted as similarity owing to the retention of plesiomorphic (primitive) characters.

PHYLOGENETIC RELATIONSHIPS IN THE CYCADS

Extant cycads comprise ten genera (*Bowenia, Ceratozamia, Cycas, Dioon, Encephalartos, Lepidozamia, Macrozamia, Microcycas, Stangeria, Zamia*) with approximately 100 species in tropical and sub-tropical regions (Greguss, 1968; Sporne, 1971a). They are typically pachycaul, unbranched, with persistent leaf bases, and are generally treated as a natural group (Bierhorst, 1971; Chamberlain, 1935; Sporne, 1971a). A detailed analysis of relationships within cycads is not available, but in this paper I am concerned only with characters that appear to define cycads as a monophyletic group.

ANALYSIS OF CHARACTERS

2.1 Girdling leaf-traces. The leaf-traces in cycads arise on the opposite side of the stem to the leaf they supply. They then girdle the stem at a slightly oblique angle before entering the leaf (Chamberlain, 1935: 88–89; Sporne, 1971a: 109). Girdling leaf-traces are not known to occur in any other gymnosperm and are interpreted as a

TABLE 1. Data matrix for characters of the Gnetales.

Character	Other Seed Plants (excluding angiosperms)	*Ephedra*	*Welwitschia*	*Gnetum*
1.1 Male gametophyte of four nuclei	+/−	−	+	+
1.2 Female gametophyte tetrasporic	−	−	+	+
1.3 Archegonia absent	−	−	+	+
1.4 Embryo with "feeder"	−	−	+	+
1.5 Ribbed pollen	−	+	+	−
1.6 Vessels	−	+	+	+
1.7 Microsporangiate and ovulate "flowers" with opposite pairs of bracteoles	−	+	+	+

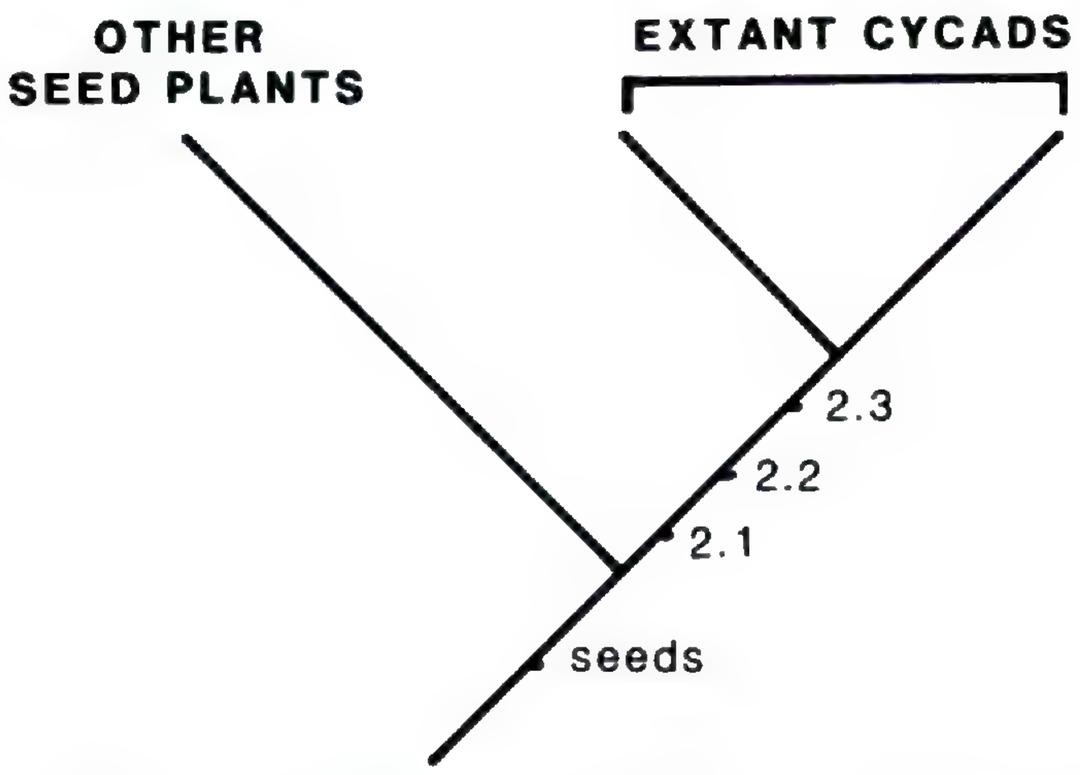


FIGURE 5. Probable synapomorphies of extant cycads. See text for further explanation.

specialized character. The traces to the cotyledons in some cycad seedlings are apparently radial (Wordsell, 1906: 153).

2.2 Simple ovulate cone. All extant genera of cycads have megasporophylls aggregated into a simple cone. In all extant genera except *Cycas* each cone terminates the activity of the apical meristem, and further growth continues sympodially by the activation of another meristem at the base of the cone stalk (Bierhorst, 1971: 373; Sporne, 1971a: 109). This mode of growth is reflected anatomically by domes of old cone vascular tissue ("cone domes") that extend across the pith. In *Cycas* only the microsporangiate plants grow in this fashion, and the ovulate plant is truly unbranched. Ovulate cones of *Cycas* only differ from those of other cycads in being indeterminate, and after the production of megasporophylls, further growth of the same apical meristem produces vegetative leaves. The simple ovulate cones of all cycads are interpreted here as a specialized feature quite different from the "compound" ovulate cones of conifers, or the "cone"-like aggregations of "flowers" in Gnetales.

2.3 Presence of cycasin. The methylazoxymethanol glycoside cycasin is present in all ten cycad genera and is not known to occur in any other gymnosperm (DeLuca et al., 1980; Moretti et al., 1983). A similar compound macrozamin is also ubiquitous in cycads and is a potential synapomorphy of the group (Moretti et al., 1983).

DISCUSSION AND INTERPRETATION

Girdling leaf-traces (character 2.1), simple ovulate cones (character 2.2), and the presence of cycasin (character 2.3) are provisionally interpreted as uniting cycads as a monophyletic group (see Fig. 5 and Table 2).

TABLE 2. Data matrix for characters of cycads.

Character	Other Seed Plants	Cycads
2.1 Girdling leaf-traces	−	+
2.2 Simple ovulate cone	−	+
2.3 Presence of cycasin	−	+

PHYLOGENETIC RELATIONSHIPS IN THE CONIFERS

The living conifers are generally treated as a natural group comprising six families: Araucariaceae, Cephalotaxaceae, Cupressaceae, Pinaceae, Podocarpaceae, and Taxodiaceae, with approximately 50 genera and 550 species (Bierhorst, 1971; Chamberlain, 1935; Sporne, 1971a). The Cupressaceae and Taxodiaceae are treated as a single family by some authors (Eckenwalder, 1976a, 1976b). A further family, the Taxaceae with five genera, sometimes is included with other conifers (Bierhorst, 1971; Chamberlain, 1935; Foster & Gifford, 1974) or sometimes separated from them (Sporne, 1971a). When included the Taxaceae is often placed with the Cephalotaxaceae in the Taxales (Greguss, 1972). Separation of the Taxaceae is based on Florin's view (1951) that the ovuliferous structures of conifers and taxads are fundamentally different (see below). A preliminary cladistic analysis of conifers was presented by Miller (1982). In this paper I deal only with the relationship between the extinct Pennsylvanian conifer *Lebachia,* extant conifers and all other seed plants. I attempt to justify the conifers sensu lato (conifers plus taxads) as a monophyletic group. Although the group is intuitively natural, a single defining character cannot be specified without invoking a series of subsidiary hypotheses. These are discussed below.

ANALYSIS OF CHARACTERS

3.1 Narrowly triangular leaves. The leaf morphology of conifers ranges from narrowly triangular to elongated needles to broad, short scales. In *Agathis* and some species of *Araucaria* and *Podocarpus,* the leaves are broad, leathery, and laminar. Despite this variability, all families, including the Araucariaceae (Stockey, 1982) and

Podocarpaceae (Buchholz & Gray, 1948), have at least some species with narrowly triangular leaves (Bierhorst, 1971, table 25-1; Dallimore & Jackson, 1948). In many conifers ontogenetic evidence is generally interpreted as indicating that helically arranged, narrowly triangular leaves are primitive within the group (Chamberlain, 1935: 358). This is particularly clear in the Cupressaceae, in which the adult foliage frequently consists of opposite and decussate, or whorled, scale-like leaves, but is also seen in other families. The ontogenetic sequence in conifers with well-developed broad, laminar leaves has never been surveyed in detail, but in *Araucaria angustifolia* (*A. brasiliensis*) the early leaves of the seedling are broadly triangular (Hill & DeFraine, 1909). In *Lebachia* the leaves are generally narrowly triangular, occasionally with bifid tips (Florin, 1951; Mapes & Rothwell, 1984; Rothwell, 1982a; Scott & Chaloner, 1983).

I interpret narrowly triangular leaves as the primitive condition in all conifers and regard all other leaf morphologies as secondary modifications of this basic type (but see Discussion and Interpretation). If this view is accepted then leaf morphology distinguishes living conifers and *Lebachia* from other seed plants, which characteristically have large megaphyllous leaves. The closest similarity to the leaves of conifers is found in *Ephedra,* but these are typically arranged in pairs or whorls of three that are joined by a sheathing base around the stem (Foster & Gifford, 1974: 523–524).

3.2 Resin canals. Resin canals occur in all conifers, although their distribution in different organs of the plant varies. In some Pinaceae they occur in the cortex of roots and stems, the wood, the leaves, and the ovulate cones. In the Araucariaceae, Cephalotaxaceae, Cupressaceae, Podocarpaceae, and Taxaceae there are typically no resin canals in the secondary xylem (Greguss, 1972) although they usually occur in other parts of the plant, and resin cells are generally present in the xylem parenchyma. Resin canals are particularly sparse in the Taxaceae, especially in *Taxus* (Chamberlain, 1935), but they do occur in the leaves of *Torreya* and the roots of *Austrotaxus* and *Taxus cuspidata* (Chamberlain, 1935: 252). Resin canals occur in Middle Pennsylvanian *Lebachia*-like conifers (Rothwell, 1982a), but lack the epithelial lining seen in many extant conifers.

It is not clear whether the "mucilage canals" of cycads, certain seed ferns, and *Ginkgo* (Bierhorst, 1971: 375; Sporne, 1971a: 168; Stewart, 1983: 253) are comparable to those of conifers. According to Bierhorst (1971: 375) the contents of these canals in cycads are partly miscible with water and do not appear to have a high terpene content. In this paper I interpret the possession of resin canals as a potential synapomorphy of conifers but closer comparisons, including developmental studies, are needed with secretory structures in other gymnosperms. I interpret the relatively sparse resin canals of *Taxus* as due to secondary loss. There is some limited ontogenetic evidence to support this conclusion. Jeffrey (1903) has reported that in *Sequoia gigantea* resin canals are present only in the secondary xylem of the first year. Resin canals also can be induced by injury in wood that otherwise lacks them (Jeffrey, 1903).

3.3 Fertile axillary shoot lacking an apical meristem. It is now widely accepted that the ovulate cones of most conifers are compound structures, the ovuliferous scale being a modified shoot bearing megasporophylls with ovules. Each ovuliferous scale is borne in the axil of a bract. This hypothesis (the polyaxial or "Brachyblast" theory, Florin, 1954) had been proposed by a succession of plant morphologists since the first half of the nineteenth century (see Coulter & Chamberlain, 1917: 245), but was advocated most strongly as a unifying concept by Florin (1951) supported by his observations on Recent and fossil conifers. On this interpretation the most primitive cones would be like those of *Cryptomeria* in which there is little fusion between the ovuliferous scale and the bract and in which the ovuliferous scale has leaf-like lobes. Cones such as those of the Cupressaceae, that show considerable fusion between the bract and ovuliferous scales, are considered relatively advanced. Ontogenetic evidence supports these ideas. In some Taxodiaceae the bract and ovuliferous scales are free when young, but not during subsequent growth (Sporne, 1971a: 141). According to the theory, each ovulate cone is a reduced "inflorescence," and hence conifers with very poorly developed cones, or with a single bract and ovuliferous scale, as in some species of *Podocarpus,* are regarded as secondarily simplified by reduction (Florin, 1951: 363–367; Wilde, 1944, fig. 40).

According to Florin (1951), only the Taxaceae cannot be accounted for in terms of the polyaxial theory, since the single terminal ovule shows no evidence of having evolved by reduction from a

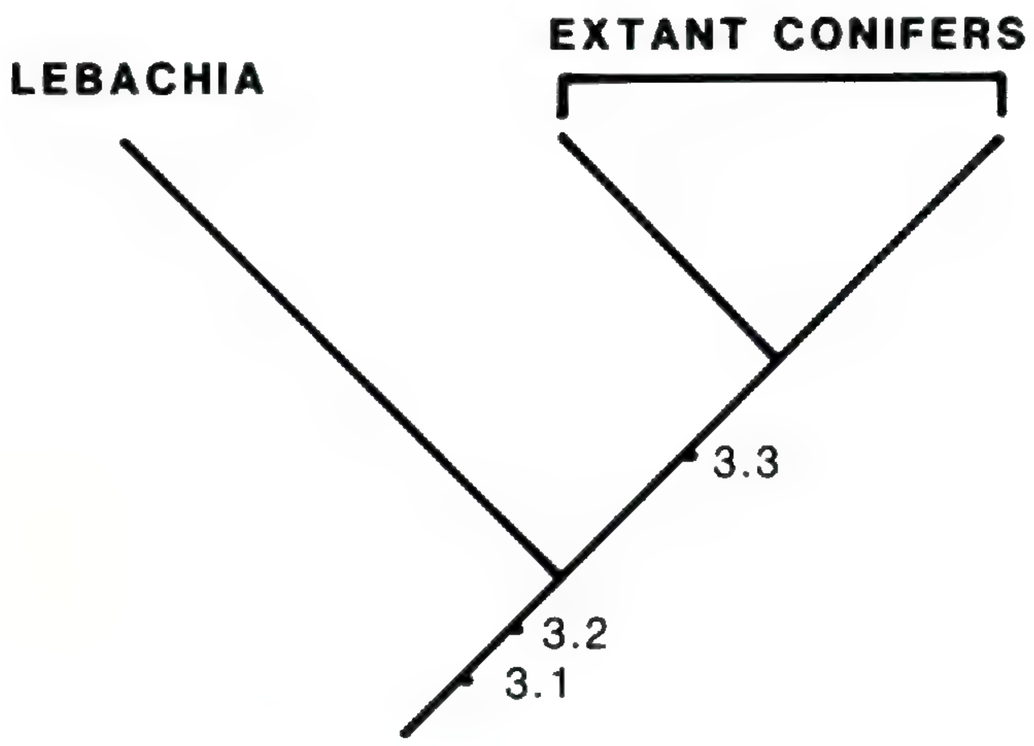


FIGURE 6. Preliminary cladogram summarizing relationships between *Lebachia* and other conifers based on the data in Table 3. See text for further explanation.

bract and ovuliferous shoot system, or from a reduced "inflorescence" (Florin, 1951: 372). Florin (1948, 1951, 1955) regarded this difference from other conifers as fundamental and indicative of a totally independent origin for the two groups. Harris (1976) argued for a closer relationship between conifers and taxads based on a plausible scenario for deriving a terminal taxad ovule from a single fertile axillary shoot. Evidence from stelar morphology is consistent with this view, and "the stelar system of Taxaceae . . . differs in no significant way from the stelar system of conifers with helical phyllotaxy" (Beck et al., 1982: 753).

I treat the Taxaceae as another family within the conifers based on their leaf morpholgy and the presence of resin canals. Like Harris (1976), I regard the terminal ovule as a secondary simplification from forms with ovuliferous scales (shoots) and bracts. Similar but less extensive simplification is interpreted as having occurred in the Podocarpaceae and Cephalotaxaceae (Florin, 1951; Wilde, 1944). This view is also implicit in those classifications of conifers that regard the Cephalotaxaceae, Podocarpaceae, and Taxaceae as closely related (Buchholz, 1934; Keng, 1975).

Modified fertile shoots in the axils of bracts or leaves also occur in cordaites, *Ginkgo,* and the Gnetales. In cordaites and *Lebachia* the apical meristem of the axillary shoot produces leaves and megasporophylls in a regular phyllotactic spiral (Florin, 1951). However, in all extant conifers the shoot apex is not differentiated (Harris, 1976: 124), and there is no regular phyllotactic spiral. I interpret this as an advance over the condition in *Lebachia* and cordaites, and therefore as a feature that unites all extant conifers.

TABLE 3. Data matrix for characters of conifers.

Character	Other Seed Plants	*Lebachia*	Extant conifers
3.1 Narrowly triangular leaves	−	+	+/−
3.2 Resin canals	+/−	+	+
3.3 Fertile axillary shoot lacking an apical meristem	+/−	−	+

DISCUSSION AND INTERPRETATION

The three characters of conifers considered here are listed in Table 3, and the resulting cladogram in Figure 6. The presence of narrowly triangular leaves and resin canals unites *Lebachia* and extant conifers as a monophyletic group. Rothwell (1982a: 18) has also pointed out that the single plane of symmetry of *Lebachia* seeds is a feature that separates them from those of other platyspermic Paleozoic gymnosperms. This could perhaps be used as a defining character of the group after further study. Within the extant conifer plus *Lebachia* group, the lack of the ovuliferous shoot apex provides a character that defines extant conifers. These conclusions may not be controversial but should be tested by a detailed cladistic analysis of extant, and well-understood fossil, conifers. For example, Beck (1981: 216) raises the intriguing alternative possibility of conifer polyphyly. Based on a consideration of Wilde's work (1944) on Podocarpaceae, he suggests that whereas most conifers may be most closely related to *Lebachia,* the Podocarpaceae may in fact be more closely related to cordaites.

PHYLOGENETIC RELATIONSHIPS IN THE GLOSSOPTERIDS

The glossopterids are a loosely defined group centered around the characteristic leaves, *Glossopteris* sensu lato, that are a dominant element in Permian and Triassic "Gondwana floras." Putative glossopterid leaves have also been described from the Jurassic of Oaxaca, Mexico (Delevoryas, 1969, but see Schopf, 1976: 26) and the Permian of Turkey (Archangelsky & Wagner, 1983). Glossopterid leaves are simple, narrowly elliptical, with a midrib and well-developed reticulate venation (Fig. 7E). The group was diverse, and a variety of different reproductive

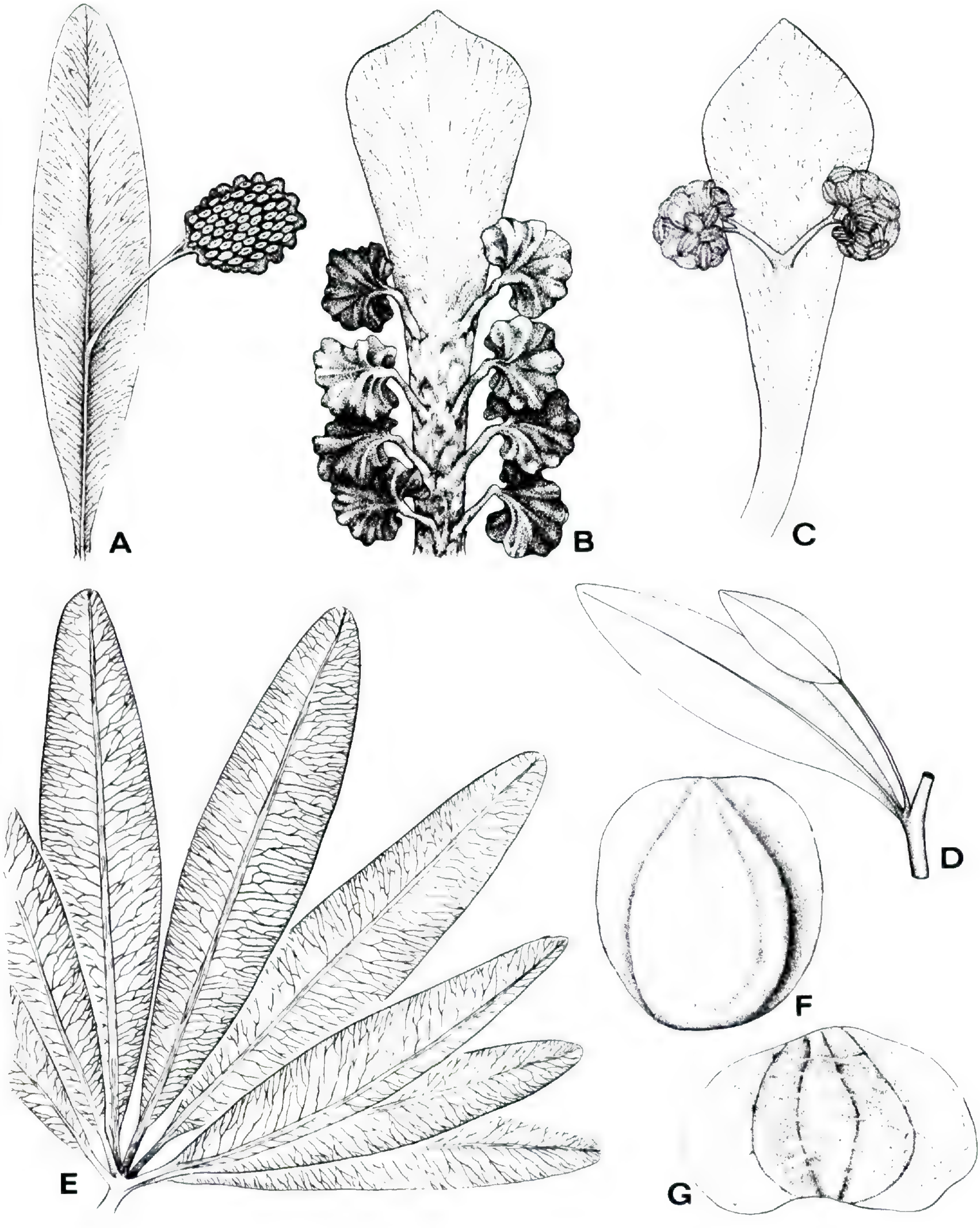


FIGURE 7. Morphology of glossopterids.—A. *Ottokaria* megasporophyll and associated leaf, redrawn from Pant (1977a, fig. 10E–G), orientation of megasporophyll based on Pant and Nautiyal (1984); ×1.—B. *Lidgettonia africana* megasporophyll, based on Thomas (1958), Surange and Chandra (1975, text-fig. 12), Schopf (1976, fig. 8D); ×1.5.—C. *Eretmonia* microsporophyll, redrawn from Surange and Chandra (1975, text-fig. 1D); ×2.—D. "*Glossopteris*" (?*Dictyopteridium*) megasporophyll in axil of a vegetative leaf, redrawn from Gould and Delevoryas (1977, fig. 1d), note that details of sporophyll attachment and sporophyll orientation are uncertain, see text for discussion; ×1.—E. *Glossopteris sastrii* leaves borne on a shoot, based on Pant and Singh (1974, text-fig. 2B–D); ×0.5.—F. *Pterygospermum raniganjense* platyspermic ovule, based on Pant and Nautiyal (1960, text-fig. 3A); ×25.—G. Pollen grain from micropyle of *P. raniganjense*, redrawn from Pant and Nautiyal (1960, text-fig. 4G); ×550.

structures have been described (Pant, 1977a; Schopf, 1976; Surange & Chandra, 1975; White, 1978). Unfortunately, many are known only as impressions in which cellular details have not been observed, and their interpretation is therefore equivocal. In this initial analysis I consider only three of the more completely understood glossopterid reproductive structures, "*Glossopteris*" (?*Dictyopteridium*, Gould & Delevoryas, 1977), *Lidgettonia* (Thomas, 1958), and *Ottokaria* (Pant, 1977a; Pant & Nautiyal, 1965).

The ovule bearing structures of most glossopterids were borne adnate to the surface of a leaf. Although they have often been reconstructed adjacent to the adaxial leaf surface (Fig. 7D), this has never been convincingly demonstrated. Glossopterid reproductive structures could be interpreted morphologically in several different ways (e.g., Retallack & Dilcher, 1981, fig. 3), but there are two main possibilities. The ovule bearing structure is either a leaf homologue (megasporophyll) or it is a modified axis (i.e., a cladode). Despite its axillary position, Gould and Delevoryas (1977) emphasized its leaf-like nature, and in this paper I treat it as a megasporophyll. This interpretation also brings the ovulate reproductive structures of glossopterids into line with those of other Mesozoic seed ferns that appear to have megasporophylls.

The anatomically preserved megasporophylls described by Gould and Delevoryas (1977) from the Late Permian of Queensland, Australia were simple, narrowly elliptical with an inrolled lamina, bearing ovules on its inner surface (Fig. 7D). Although Gould and Delevoryas provided some evidence to suggest that the ovule bearing surface faced the subtending leaf, the interpretation remains equivocal and at variance with the reconstruction of *Ottokaria* by Pant and Nautiyal (1984, see below). The gross form of the Queensland material is similar to *Dictyopteridium* described from an impression (Gould & Delevoryas, 1977: 397; Surange & Chandra, 1975). The interior of the structure was filled by a delicate network of filaments, or plates of cells, between the ovules. Based on clusters of *Arberiella* pollen sacs in the Queensland chert, Gould and Delevoryas (1977) suggested that the microsporangiate organs of their plant were of the *Eretmonia* or *Glossotheca* type (Fig. 7C). From other localities *Eretmonia* and *Glossotheca* are known to consist of a fertile portion (interpreted here as a microsporophyll) adnate to a leaf. The microsporophyll consisted of a bifurcated axis, each branch of which bore numerous *Arberiella* microsporangia. Pollen was bisaccate (*Protohaploxypinus*), with numerous distinct striations on the body of the grain oriented at 90° to the distal suture (Fig. 7G).

Lidgettonia africana (Fig. 7B) was described by Thomas (1958) from the Upper Permian of South Africa. It consists of a sterile leaf with an adnate megasporophyll. The megasporophyll differs from that in Gould and Delevoryas' material in bearing about eight fertile "cupules" on slender stalks adnate to the lamina of the subtending leaf. Each "cupule" consisted of an expanded disc, which is thought to have borne ovules on its lower surface. Thomas (1958) interpreted these discs as peltate, but Schopf (1976: 45–48) has shown that the stalk was attached laterally, as in the Indian species *L. mucronata* (Surange & Chandra, 1975). *Arberiella* pollen sacs and microsporophylls of the *Eretmonia* type are associated with the *Lidgettonia* fructifications (Schopf, 1976: 50; Thomas, 1958), but no information is available on the pollen. In this study I assume that it was of the *Protohaploxypinus* type.

Ottokaria (Pant, 1977a; Pant & Nautiyal, 1965, 1984) from the Permian of India is preserved as compressions from which some cellular details are known. The megasporophyll was adnate to the upper surface of a leaf and expanded distally to form a "spoon-shaped" head with sterile marginal lobes, bearing ovules on the concave surface (Fig. 7A). Contrary to Gould and Delevoryas' interpretation of the Queensland material, the ovule bearing surface faced away from the subtending leaf (Pant & Nautiyal, 1984). The ovules are similar to the dispersed ovule genera *Pterygospermum* (Fig. 7F) and *Platycardia* (Pant, 1977a; Pant & Nautiyal, 1960). *Protohaploxypinus* pollen ("*Striatites*," Pant, 1977a) occurs in the micropyles of these dispersed ovules. Apart from the inference that they contained *Protohaploxypinus* pollen, the microsporophylls or microsporangia of *Ottokaria* are unknown. In this paper they are assumed to have been similar to *Eretmonia*.

ANALYSIS OF CHARACTERS

4.1 Glossopterid leaves. The leaves of all three genera are narrowly elliptical, with reticulate venation. The leaves are distinctive, not known to occur in any other group of gymnosperms, and are interpreted as a specialized char-

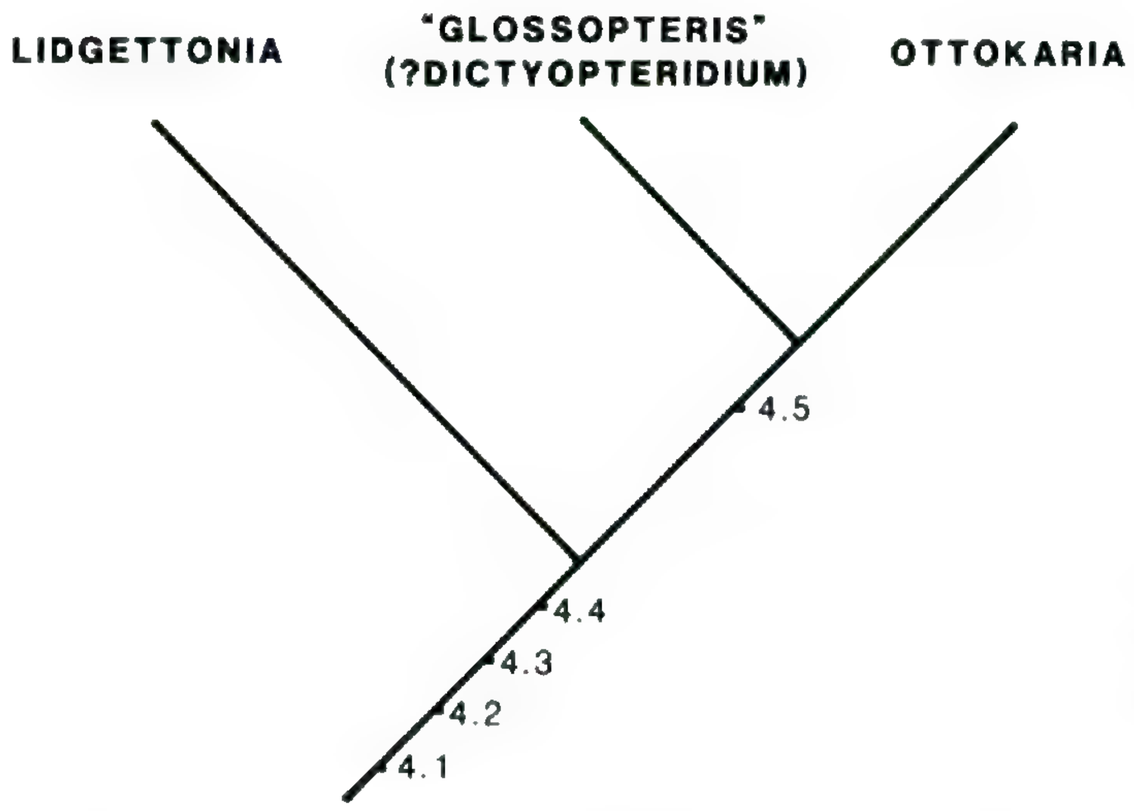


FIGURE 8. Preliminary cladogram summarizing relationships between *Lidgettonia*, "*Glossopteris*" (?*Dictyopteridium*), and *Ottokaria* based on the data in Table 4. See text for further explanation.

acter. The closest similarity in venation occurs in leaflets of *Caytonia* (*Sagenopteris*), but this general pattern of reticulate venation is also widespread in ferns and other groups (Alvin & Chaloner, 1970).

4.2 Megasporophylls adnate to a subtending leaf. The megasporophylls in all three genera are adnate or closely adjacent to the subtending leaf. This arrangement is unknown in any other group of seed plants and is interpreted as a specialized character.

4.3 Microsporophylls adnate to a subtending leaf. Glossopterid microsporophylls from several localities (Pant, 1977a) are borne adnate to the subtending leaf (Gould & Delevoryas, 1977). This basic arrangement is apparently general in glossopterid plants and is assumed (although not known) to be present in the three glossopterids considered here. It is not known to occur in any other group of seed plants and is interpreted as a potential glossopterid synapomorphy.

4.4 Striate bisaccate pollen. Bisaccate pollen with a transverse distal sulcus, and longitudinal striations on the body of the grain, is thought to be general in glossopterids. It occurs rarely in other groups of gymnosperms and some conifers (see also *Nipurdia,* Pant & Basu, 1979). It is intepreted as a specialized character.

4.5 Simple megasporophyll. In "*Glossopteris*" (?*Dictyopteridium*) and *Ottokaria,* the ovules are borne on the surface of a simple laminar structure, interpreted here as a simple megasporophyll. Megasporophylls of *Cycas* are similar, but are not adnate to a subtending leaf, and bear ovules only on the margin rather than over the lamina surface. In *Lidgettonia* the presence of several ovule bearing structures suggests that the adnate megasporophyll was pinnate rather than simple as in "*Glossopteris*" (?*Dictyopteridium*) and *Ottokaria.* Pinnate megasporophylls occur in the following seed ferns: *Callistophyton,* peltasperms, corystosperms, and *Caytonia*; and are therefore interpreted here as primitive within the glossopterids. The simple lamina is interpreted, conversely, as a specialized feature that unites "*Glossopteris*" (?*Dictyopteridium*) and *Ottokaria.*

DISCUSSION AND INTERPRETATION

The data matrix for the five characters of glossopterids is given in Table 4 and the resulting cladogram in Figure 8. Glossopterids are defined as monophyletic by four characters (4.1–4.4). Within this group *Ottokaria* and "*Glossopteris*" (?*Dictyopteridium*) are more closely related based on their simple axillary megasporophylls. These conclusions, and the assumptions made, need to be tested by further work. As pointed out by Pant (1977a), there is no evidence to support the suggestion of Surange and Chandra (1975) that the

TABLE 4. Data matrix for characters of glossopterids.

Character	Other Seed Plants	*Lidgettonia*	*Glossopteris/ Dictyopteridium*	*Ottokaria*
4.1 Glossopterid leaves	−	+	+	+
4.2 Megasporophylls adnate to a subtending leaf	−	+	+	+
4.3 Microsporophylls adnate to a subtending leaf	−	+	+	+
4.4 Striate bisaccate pollen	+/−	+	+	+
4.5 Simple megasporophyll	+/−	−	+	+

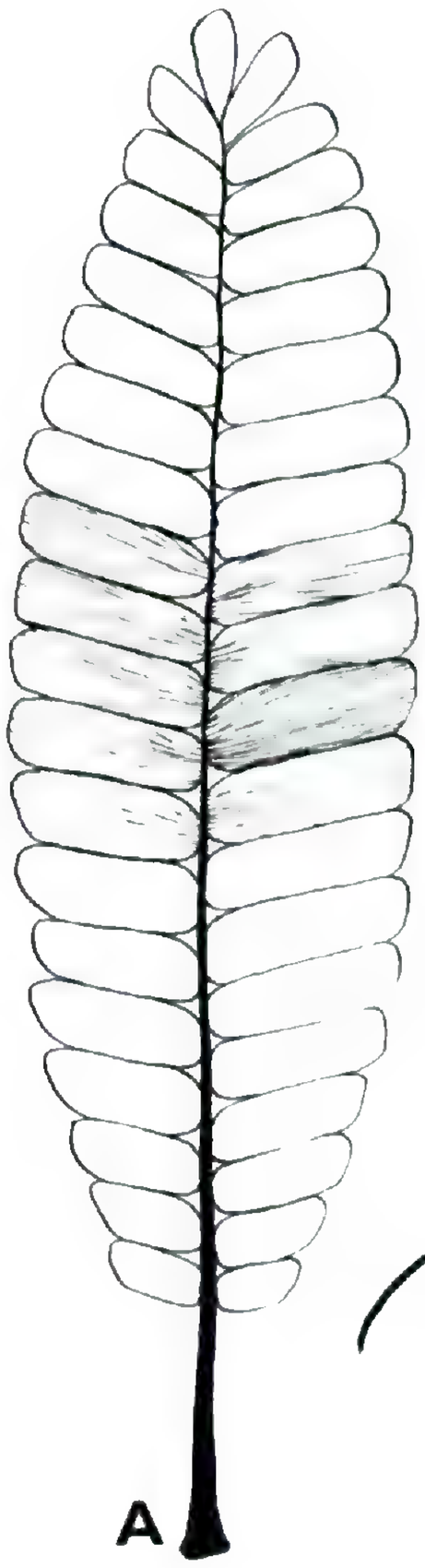
glossopterids sensu lato should be divided into "pteridospermous" and "glossopterid" forms.

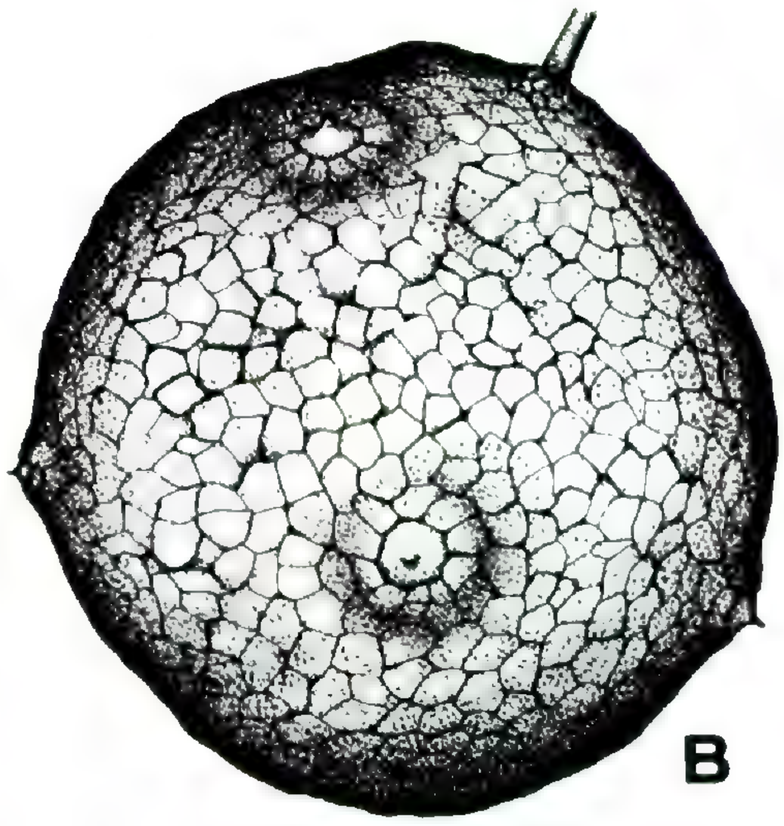
Phylogenetic Relationships in the Bennettitales

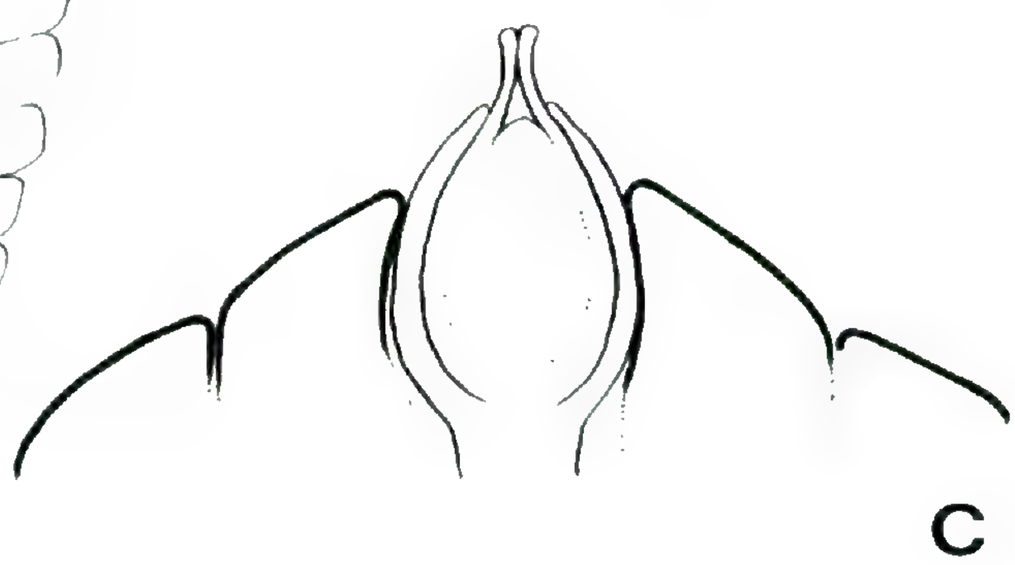
The Bennettitales are diverse and abundant plants in Upper Triassic to Upper Cretaceous floras. The leaves may be simple (*Nilssoniopteris*) or, more typically, pinnate, with parallel, occasionally dichotomous veins in the pinnae. In *Dictyozamites* the veins are reticulate. The leaves are superficially like those of cycads but can usually be distinguished by characters of gross form and always by their characteristically cutinized syndetocheilic (paracytic) stomata (Fig. 11C) that contrast with the haplocheilic (anomocytic) stomata of true cycads (Harris, 1932a; Thomas & Bancroft, 1913). Bennettitalean microsporophylls or ovules were aggregated into flower-like heads, usually surrounded by a "perianth" of bracts. The "flowers" were unisexual (monosporangiate) or bisexual (bisporangiate). In all Bennettitales the ovules were orthotropous, with two integuments joined to the nucellus only at the chalaza (see interpretation of *Vardekloeftia* and *Bennetticarpus crossospermus* below; also characters 9.19, 9.22). Distally, the inner integument generally formed an elongated micropylar tube. The ovules were crowded together into heads and individually were not subtended by any other organ. In most compressions of bennettitalean ovules cuticles are obtained from the outer, and usually the inner, surface of the inner integument, the micropylar tube, and the surface of the nucellus; but there is no maceration resistant megaspore membrane (Harris, 1932b, 1954, 1969). The ovules were separated by sterile interseminal scales, which had a single vascular bundle. The morphological nature of these interseminal scales is uncertain, but the structure of *B. crossospermus* described by Harris (1932b) provides evidence to support Seward's view (1913: 118, 1917: 403) that they are homologous with ovules (see also Delevoryas, 1968: 141, interpreted here as bitegmic, p. 764). In *B. crossospermus* (Fig. 9E, F) the elongated micropylar tube passed through the center of a thickly cutinized "micropylar plate" very similar to the flattened cutinized apices of the interseminal scales in the same gynoecium (Fig. 9E). This suggests that the ovules and interseminal scales may be homologous and that the scales "are formed by the diverted development of seed initials" (Harris, 1932b: 116). Studies of ovule development in *Williamsonia* (Sharma, 1974) also support this idea. There is some evidence that *B. crossospermus* is associated with *Pterophyllum ptilum* leaves (Fig. 9D; Harris, 1932b: 103), but the morphology of the gynoecium is too poorly known to assess the relationships of the plant in more detail. In this paper relationships between 11 of the better understood bennettitalean taxa are considered (Table 5).

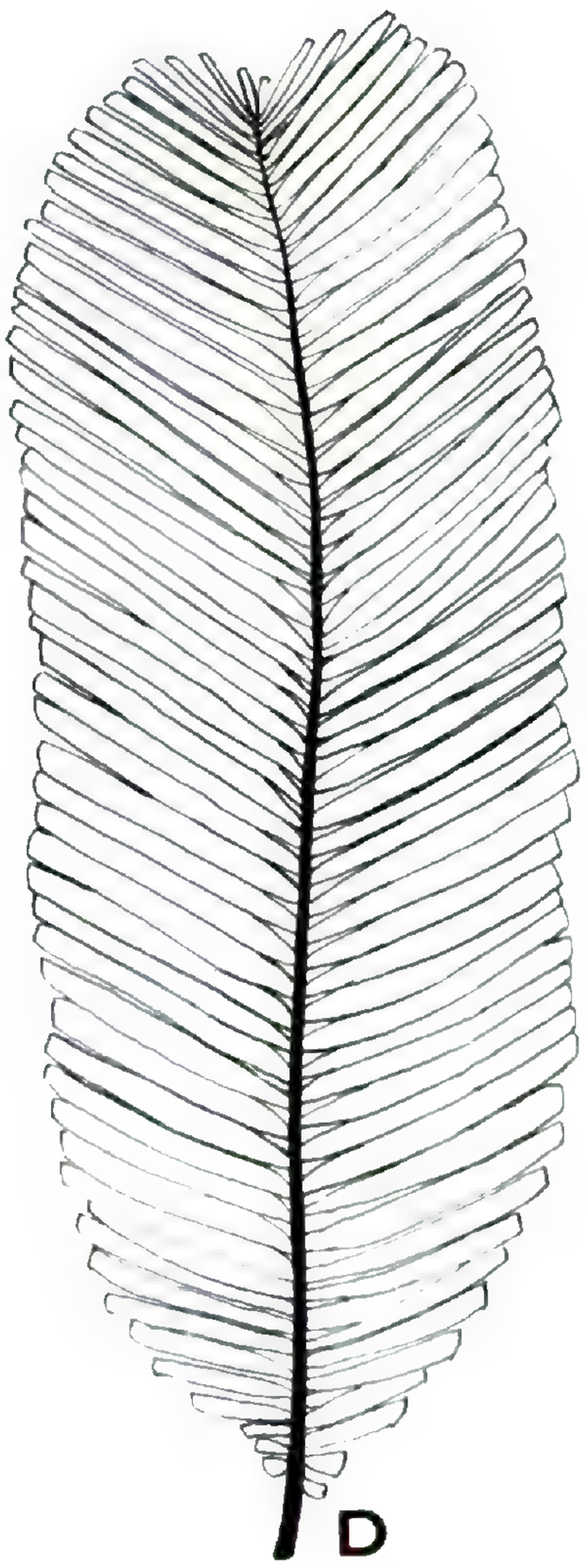
Vardekloeftia is a genus erected by Harris (1932b) for two species of spherical, bennettitalean, ovulate heads from the Rhaetic of Greenland. Each head was composed of flattened, bilaterally symmetrical ovules separated by numerous interseminal scales. The ovules were relatively few (two to 20), and relatively large (5–7 mm long), compared to those of most Bennettitales. They also were unusual in having an outer cutinized layer (the "cupule," Harris, 1932b, interpreted here as the outer integument) surrounding the inner integument in an identical position to the "micropylar plate" of *B. crossospermus*. Two very similar species have been described, *V. conica,* and the more completely known *V. sulcata*. In *V. sulcata* (Fig. 9B, C), each head contained two to six seeds. In young ovules the cutinized layer outside the inner integument formed a flattened plate through the center of which the micropyle projected. At this stage the outer layer (outer integument) was very similar to the micropylar plate of *B. crossospermus* but was less substantial at maturity. *Vardekloeftia sulcata* is associated with *Pterophyllum kochi* leaves (Fig. 9A; Harris, 1932b: 111), but the microsporangiate structures are unknown.

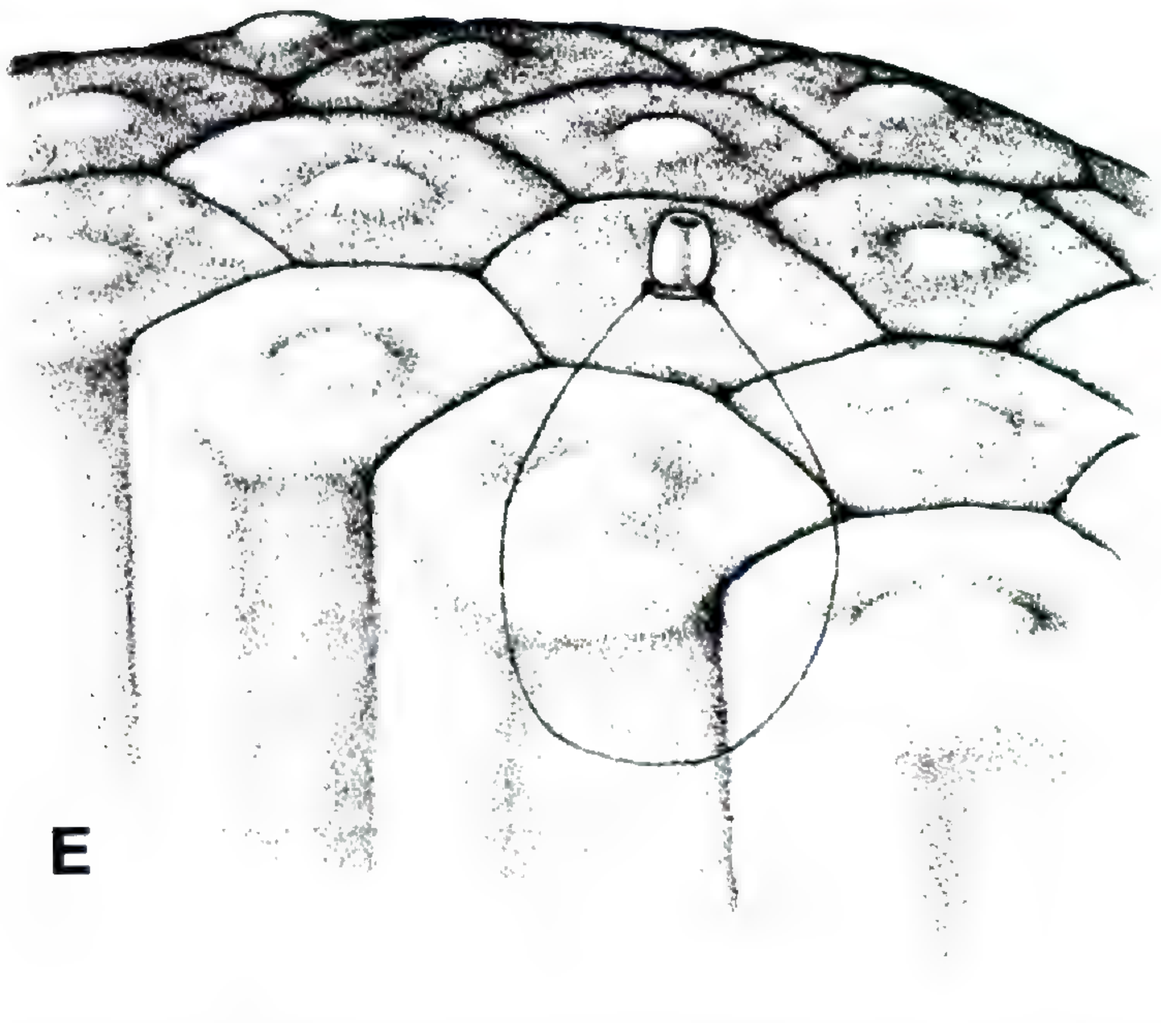
With the exception of *Vardekloeftia* all other bennettitalean taxa considered in this paper have more ovules in their megasporangiate "flowers" and a well-differentiated "perianth." The basic structure is illustrated by two very similar species, *Williamsonia harrisiana* (Bose, 1968) and *W. sewardiana* (Sahni, 1932b), both based on silicified material from the Upper Jurassic of the Rajmahal Hills, India. These species had a conical or hemispherical receptacle bearing ovules and interseminal scales all over the surface (Fig. 10A). *Williamsonia sewardiana* is thought to have been attached to *Bucklandia indica* stems that bore *Ptilophyllum* cf. *cutchense* leaves (Sahni, 1932b: 10). Both species were apparently unisexual (monosporangiate). Although microsporangiate "flowers" have been described from the Rajmahal Hills (Bose, 1967; Sharma, 1969; Sith-











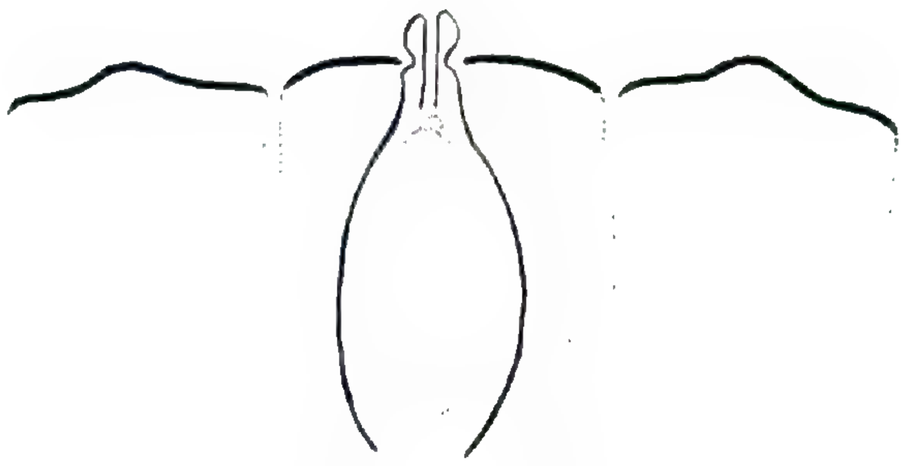
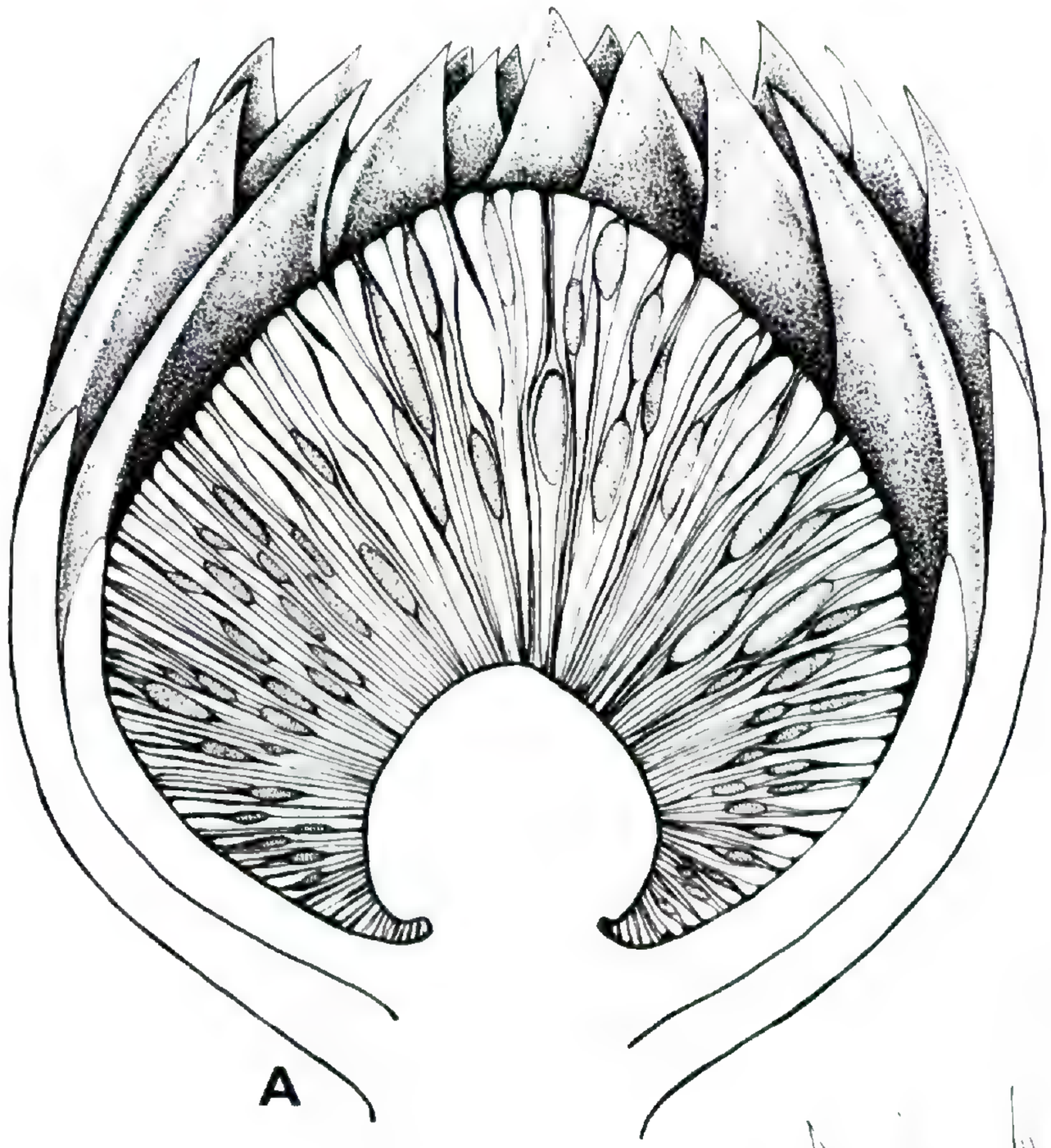
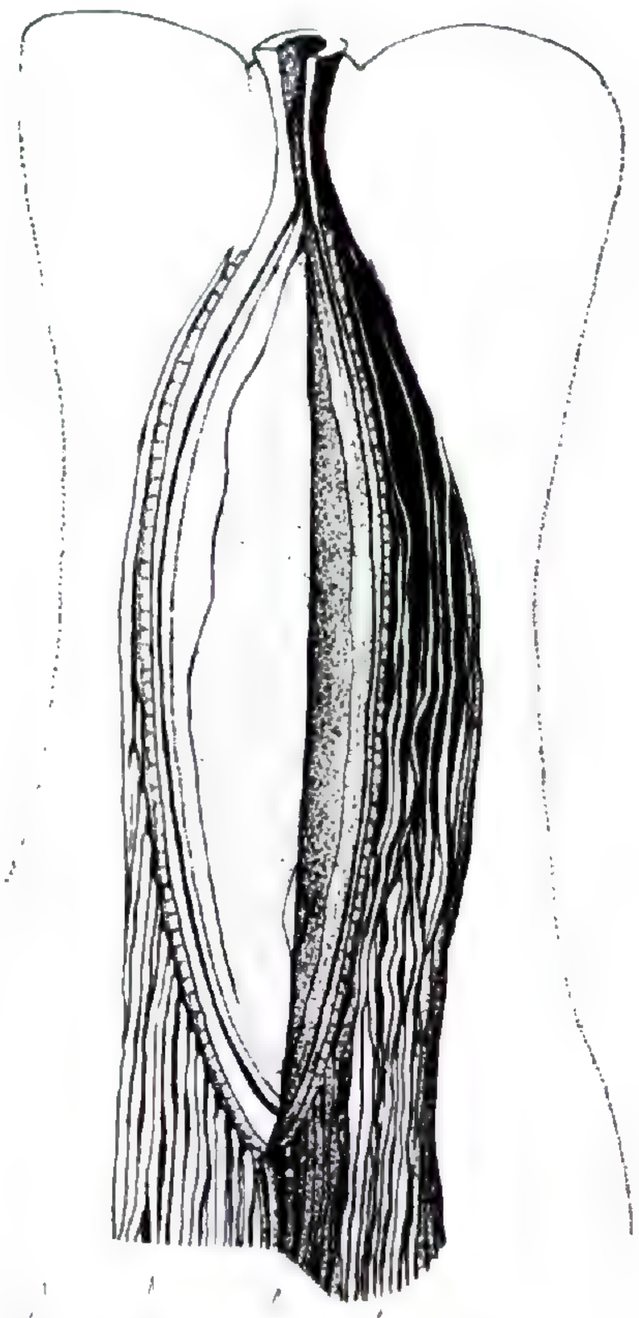


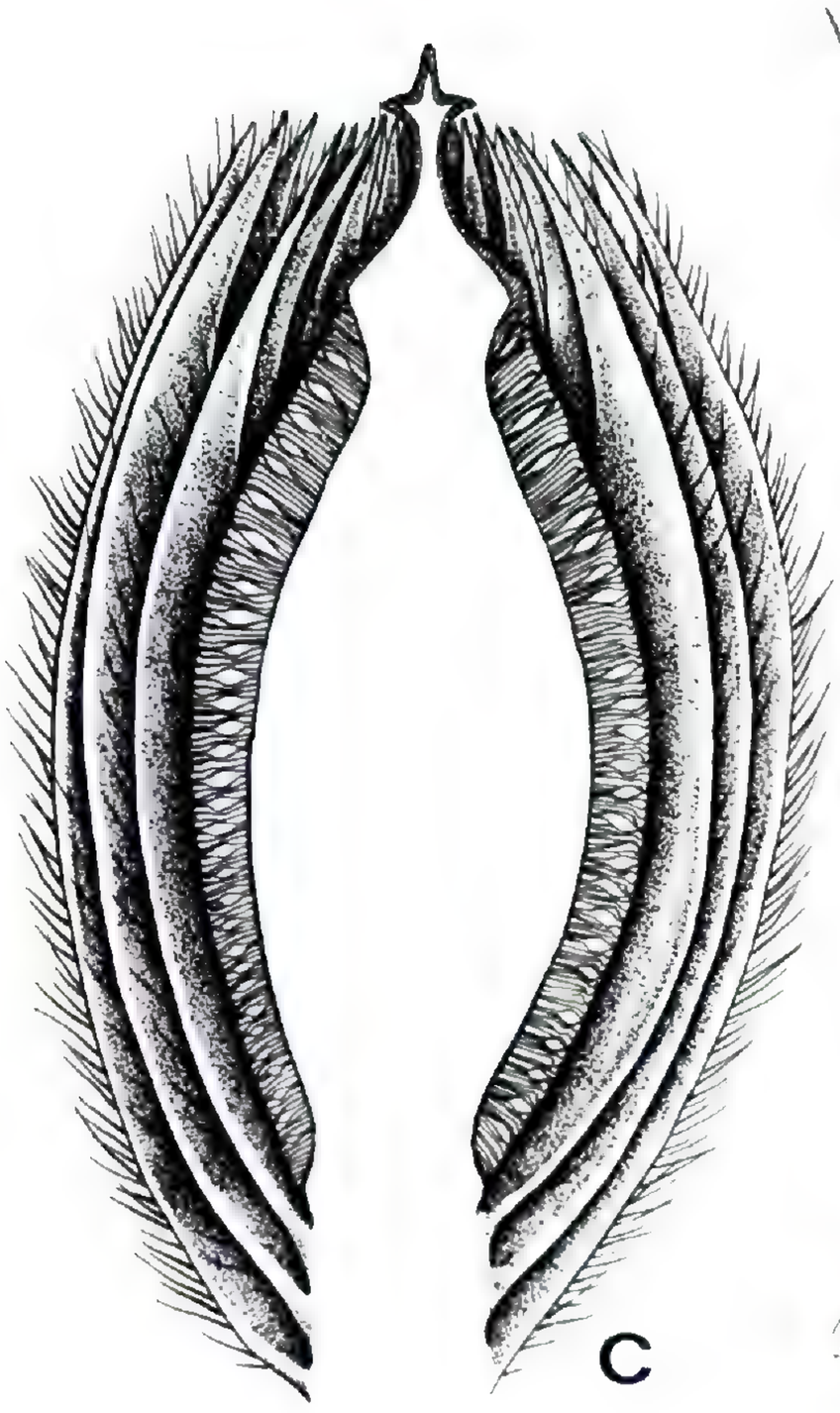
FIGURE 9. Morphology of the *Vardekloeftia* and *Bennetticarpus* plants.—A. *Pterophyllum kochii,* based on Harris (1932b, fig. 29); ×0.5.—B. *V. sulcata,* spherical head composed of ovules and interseminal scales, based on Harris (1932b, pl. 15, fig. 1, pl. 17, figs. 1, 2, pl. 18); ×2.—C. *Vardekloeftia,* longitudinal section through ovule, redrawn from Harris (1932b, fig. 50E); ×5.—D. *Pterophyllum ptilum,* based on Harris (1932b, fig. 30I); ×0.5.—E. *B. crossospermus,* outer surface of interseminal scales showing position of ovule, based on Harris (1926, pl. 11; 1932b, fig. 48J); ×10.—F. *B. crossospermus,* longitudinal section through ovule, redrawn from Harris (1932b, fig. 50C); ×10.

TABLE 5. Isolated organs of the better known Bennettitales.

Locality	Stem	Ovulate Flower	Microsporangiate Flower	Leaf	Primary Reference
E Greenland (U. Triassic–L. Jurassic)	?	*Vardekloeftia sulcata*	?	*Pterophyllum kochii*	Harris, 1932b
India, Rajmahal Hills (Jurassic)	*Bucklandia indica*	*Williamsonia sewardiana*	?	*Ptilophyllum* cf. *cutchense*	Sahni, 1932b
	?	*Williamsonia harrisiana*	?	?	Bose, 1968
New Mexico (U. Cretaceous)	*Monanthesia magnifica*	*Monanthesia magnifica*	?	?	Delevoryas, 1959
Sweden & E Greenland (U. Triassic–L. Jurassic)	*Wielandiella angustifolia*	*Wielandiella angustifolia*	?*Hydropterangium marsilioides*	*Anomozamites minor*	Harris, 1932b
U.K., Yorkshire (M. Jurassic)	*Bucklandia gigas*	*Williamsonia gigas*	*Weltrichia sol*	*Zamites gigas*	Harris, 1969
	Bucklandia pustulosa	*Williamsonia hildae*	*Weltrichia whitbiensis*	*Ptilophyllum pectinoides*	Harris, 1969
	cf. *Bucklandia pustulosa*	*Williamsonia leckenbyi*	*Weltrichia pecten*	*Ptilophyllum pecten*	Harris, 1969
	slender (see Harris, 1969: 147)	*Williamsoniella coronata* (bisexual)	*Williamsoniella coronata* (bisexual)	*Nilssoniopteris vittata*	Harris, 1969
	?	*Williamsoniella lignieri* (bisexual)	*Williamsoniella lignieri* (bisexual)	*Nilssoniopteris major*	Harris, 1969
South Dakota (L. Cretaceous)	*Cycadeoidea* sp.	*Cycadeoidea* sp. (bisexual)	*Cycadeoidea* sp. (bisexual)	?*Zamites*	Crepet, 1974







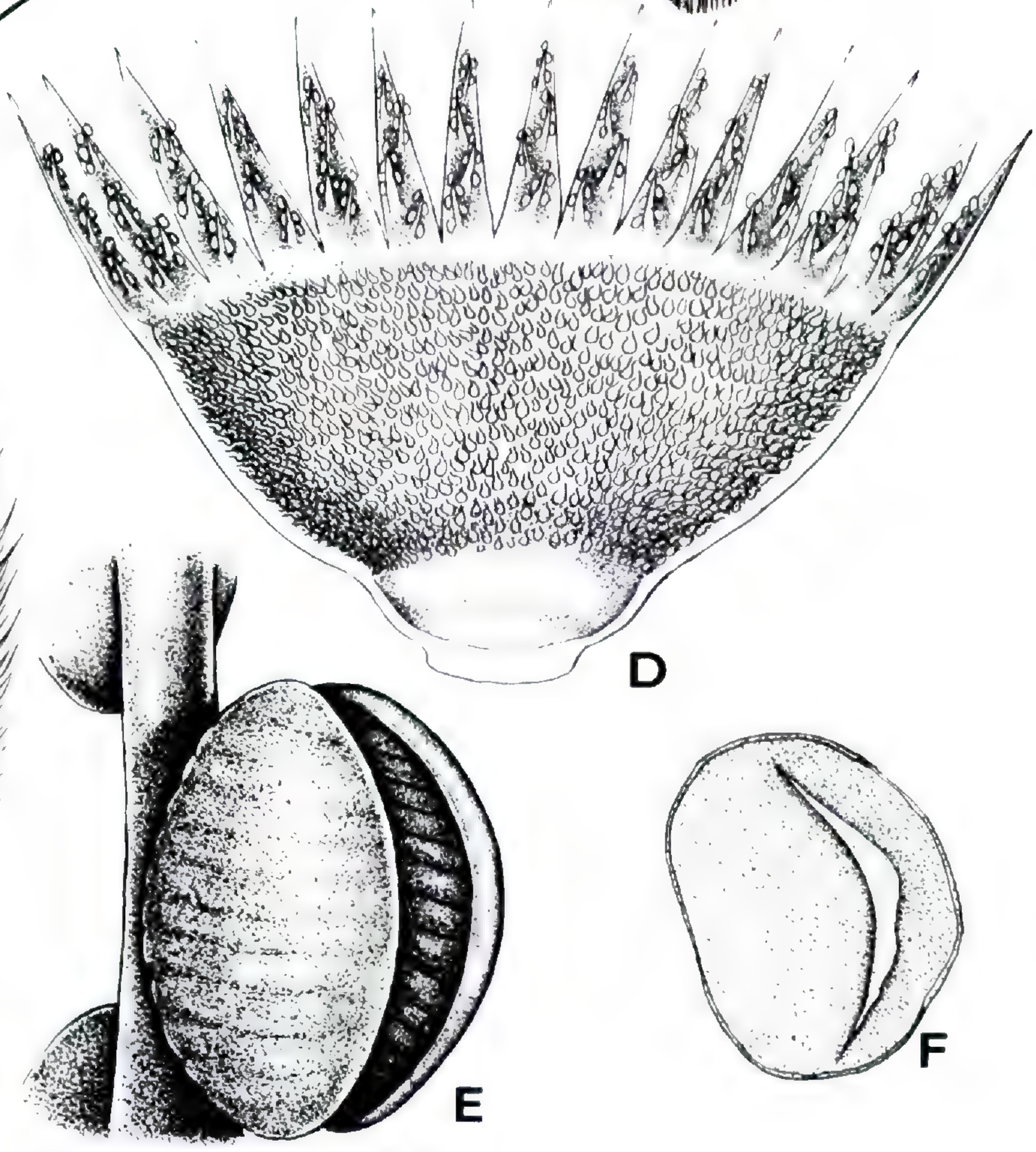


FIGURE 10. Morphology of Bennettitales.—A. *Williamsonia harrisiana*, longitudinal half section of "flower," based on Bose (1968, pl. 1, figs. 8, 9); ×1.5.—B. *Bennettites albianus*, cutaway section through an ovule, based on Stopes (1918, text-figs. 13, 14); ×15.—C. *Williamsonia gigas*, longitudinal half section of young "flower," based on Harris (1969, fig. 56) and Hill et al. (in press); ×1.—D. *Weltrichia sol*, longitudinal half section through microsporangiate "flower," redrawn from Harris (1969, fig. 69E); ×0.5.—E. *W. sol*, detail of synangium, based on Harris (1969, fig. 69F); ×10.—F. *W. sol* pollen grain, redrawn from Harris (1969, fig. 69A); ×600.

oley & Bose, 1953, 1971), the microsporangiate structures of both species, and the vegetative parts of *W. harrisiana,* are unknown.

Monanthesia described from the Upper Cretaceous Mesaverde Formation of New Mexico (Delevoryas, 1959) is similar to *Williamsonia sewardiana* and *W. harrisiana.* The "flowers" were monosporangiate and borne on long, slender peduncles in the axil of almost every leaf. The receptacle was conical and covered with ovules and interseminal scales. The microsporangiate "flowers" and pollen are unknown.

Four species of *Williamsonia* have been described based on compressions from the Middle Jurassic of Yorkshire, *W. gigas, W. hildae, W. leckenbyi,* and *W. himas* (Table 5; Harris, 1969). The first three are the best understood as "whole" plants, and *W. himas* is not considered further in this review. *Williamsonia gigas* (Fig. 10C) has been linked to the leaves *Zamites gigas* and the microsporangiate "flowers" *Weltrichia sol* (Fig. 10D, E; Harris, 1969: 163). *Williamsonia hildae* has been linked with the leaves *Ptilophyllum pectinoides,* the microsporangiate "flowers" *Weltrichia whitbiensis,* the "perianth" bracts *Cycadolepis hypene,* and the stem *Bucklandia pustulosa* (Harris, 1969: 172). *Williamsonia leckenbyi* has been linked to the leaves *Ptilophyllum pecten* and the microsporangiate "flowers" *Weltrichia pecten* (Harris, 1969: 170) (Table 5). The structure of the ovulate "flowers" in all three species is basically similar to that in *Williamsonia harrisiana* and *Williamsonia sewardiana.* The Yorkshire species differ however in the presence of a distinct sterile "corona" above the level at which ovules are borne. The corona is formed from the receptacle and interseminal scales (Fig. 10C; C. R. Hill, pers. comm.; Harris, 1969: 129). The microsporangiate "flowers" of the three plants also are basically similar. *Weltrichia sol* consisted of a whorl of up to 30 "rays" (interpreted here as microsporophylls) more or less fused proximally into a cup-like structure. The inner surface of the cup bore large numbers of "resinous sacs" and the free parts of the microsporophylls bore two-valved synangia (Fig. 10E), each valve of which contained several microsporangia. The pollen was psilate and monosulcate (Fig. 10F). In *Weltrichia sol* (Fig. 10D) there were about 30 microsporophylls, and the synangia were borne alternately on short fertile appendages that projected from the inner surface of the microsporophyll. Comparison with the microsporophylls of *Cycadeoidea* suggests that these appendages are fertile pinnae. Each valve of the synangium contained about 12–15 microsporangia. In *Weltrichia pecten* and *Weltrichia whitbiensis* there were between ten and 20 microsporophylls, each with sessile synangia in two rows on their inner surface.

Wielandiella angustifolia from the Rhaetic of Scania, southern Sweden (Nathorst, 1909), and Greenland (Harris, 1932b) had monosporangiate "flowers" (Harris, 1932b: 90–91). The ovulate "flowers" are similar to those of *Williamsonia gigas, Williamsonia leckenbyi,* and *Williamsonia hildae* and have a distal sterile corona. The microsporangiate flowers are poorly understood and require restudy (Lundblad, 1950: 73), but the "palisade rings" described at the base of the "flower" by Nathorst (1909) are similar to *Hydropterangium marsilioides* (Lundblad, 1950). The leaves of *Wielandiella angustifolia* are thought to be *Anomozamites minor.*

Two similar species of *Williamsoniella* are known as compressions from the Middle Jurassic of Yorkshire (Harris, 1944, 1969, 1974). Both were bisporangiate (bisexual) "flowers" (Fig. 11A, D). A whorl of bracts formed a "perianth" around a whorl of about 12 laterally compressed, wedge-shaped microsporophylls. Each microsporophyll bore two or three pairs of short fertile appendages on the adaxial surface (interpreted as fertile pinnae), each of which bore a single two-valved synangium containing pollen sacs with psilate monosulcate pollen. At the center of the "flower" the receptacle bore ovules and interseminal scales and was expanded distally into a terminal sterile corona. The two species, *Williamsoniella lignieri* and *Williamsoniella coronata* (Fig. 11D), are linked with *Nilssoniopteris major* and *N. vittata* (Fig. 11B, C), respectively (Harris, 1969: 146, 149). *Williamsoniella lignieri* was larger than *W. coronata* and generally is less well understood. "Perianth" bracts are associated with the "flower" but have not been seen attached.

Many species of *Cycadeoidea* have been described from a wide range of Upper Jurassic and Lower Cretaceous localities in the Northern Hemisphere (Crepet, 1974; Stewart, 1983; Wieland, 1906, 1916), but all show a basically similar structure. *Cycadeoidea* was pachycaul, with short, stout trunks and helically arranged leaf bases that probably bore *Zamites*-like leaves (Seward, 1917; Wieland, 1906: 87). The "flowers" were bisporangiate (bisexual) (Fig. 11E) and borne on short pedicels in leaf axils. They did not project beyond the persistent leaf bases. There was a perianth of

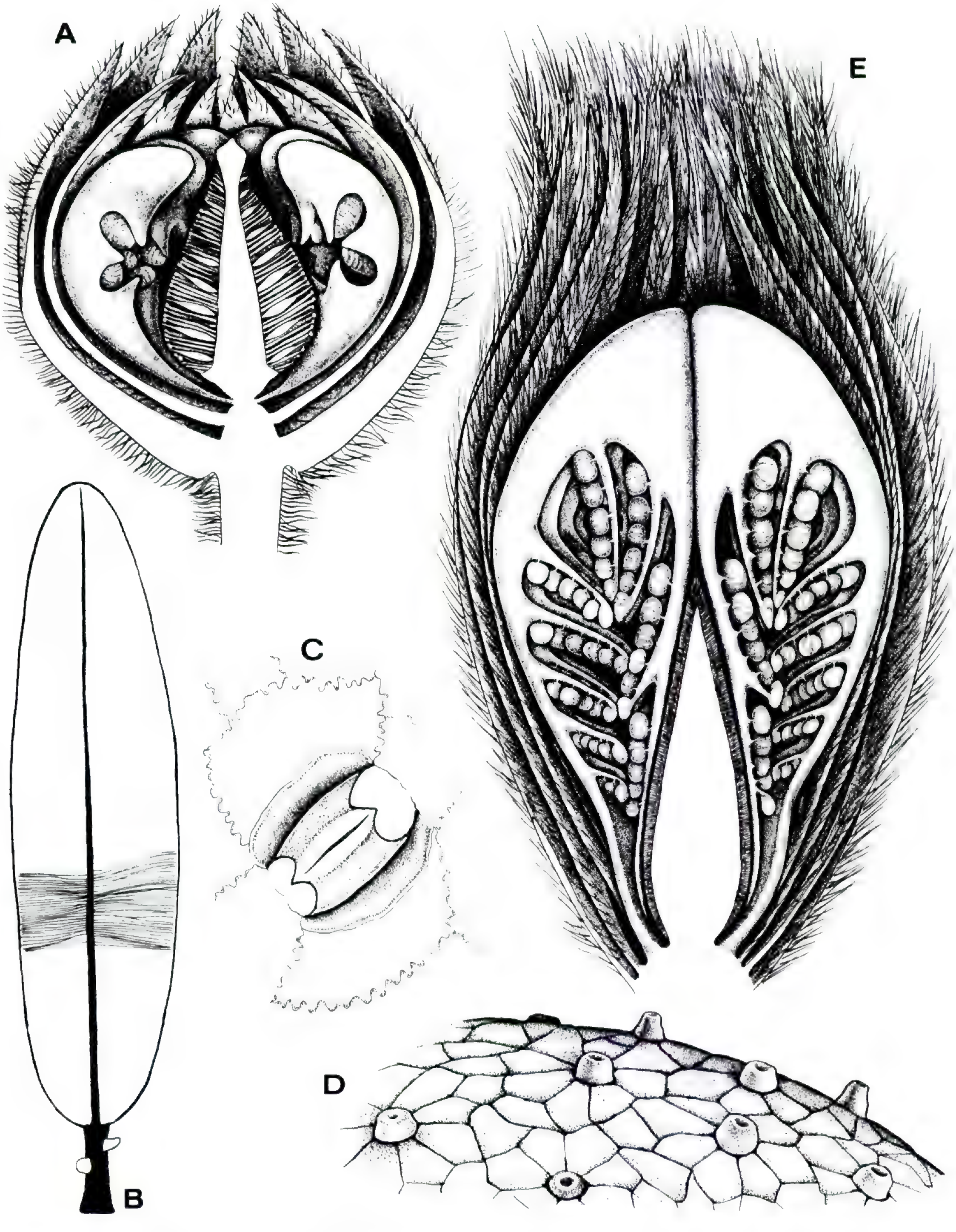


FIGURE 11. Morphology of Bennettitales.—A. *Williamsoniella coronata,* longitudinal half section through "flower," based on Harris (1944, fig. 1); × 3.—B. *Nilssoniopteris vittata,* redrawn from Harris (1969, fig. 32A), an unusual specimen showing two lateral pinnae at the base; ×1.—C. *N. vittata,* detail of stoma showing paracytic guard cells and sinuous anticlinal flanges, based on Harris (1969, fig. 32D); ×1,000.—D. *W. coronata,* surface of immature "gynoecium" showing micropyles and interseminal scales, based on Harris (1969, fig. 62F); ×50.—E. *Cycadeoidea* sp., longitudinal half section through "flower," based on Wieland (1906, fig. 88) and Crepet (1974, pl. 61, fig. 21); ×1.5.

helically arranged outer bracts surrounding approximately 20 microsporophylls. These were fused proximally into a shallow cup but were pinnate distally and compressed laterally. Two rows of appendages (pinnae) were borne adaxially, each with a row of about six kidney-shaped synangia. The synangia contained eight to 20 tubular sporangia and produced psilate, monosulcate, granular-walled pollen (Crepet & Zavada, pers. comm.). Towards their apices the microsporophylls were incurved, with their abaxial surface against a conical or domed receptacle covered with ovules and interseminal scales, and showing no sign of a corona. Delevoryas (1963, 1968) and Crepet (1972, 1974) both support the view that the microsporophylls never opened to become fully expanded as Wieland (1906) supposed.

ANALYSIS OF CHARACTERS

6.1 Interseminal scales. Interseminal scales occur in all Bennettitales considered in this analysis. They are not known to occur in any other seed plant, and following Harris (1932b) I interpret them as developing from ovule primordia (see characters 9.19, 9.22). They are regarded here as a specialized character.

6.2 Guard-cells, paracytic and heavily cutinized. The stomata of all Bennettitales are paracytic and interpreted as ontogenetically syndetocheilic (Harris, 1932a; Thomas & Bancroft, 1913). This is sufficient to distinguish them from the stomata of most other gymnosperms except *Gnetum, Welwitschia,* and some conifers (Scott & Chaloner, 1983). However, the guard-cells of the Bennettitales also have characteristic, heavily cutinized, outer periclinal walls and dorsal anticlinal flanges. This feature occurs in leaves with both sunken and superficial stomata but is not thought to occur in other gymnosperms (Harris, 1932a: 94–108).

6.3 Ovulate heads with numerous ovules. All of the Bennettitales considered in this study have numerous (more than 100) ovules in their megasporangiate heads. In *Vardekloeftia,* although only two to six seeds develop per head, there are a large number of interseminal scales that are interpreted as sterile ovule primordia. No other gymnosperms (except the Vojnovskyaceae and Ruflorinaceae, Meyen, 1984) have such a large number of ovules clustered together, and I interpret this as a potential synapomorphy of the Bennettitales.

6.4 Bivalved synangia. Most bennettitalean microsporophylls have the microsporangia within bivalved synangia. Although the microsporangia of *Vardekloeftia, Williamsonia sewardiana, W. harrisiana,* and *Monanthesia* are unknown, the bivalved condition is interpreted here as general in the Bennettitales. In many seed plants (e.g., conifers, cycads) the microsporangia are not in synangia; where they do occur (e.g., *Caytonanthus,* medullosans, and Gnetales), they are not arranged to form a bivalved capsule. Here I interpret the bivalved synangia of Bennettitales as a specialized condition, although it should be noted that they do not occur in all bennettitalean pollen organs (e.g., *Leguminanthus siliquosus* Kräusel & Schaarschmidt, 1966).

6.5 "Perianth" of helically arranged bracts. All of the Bennettitales considered in this study, with the exception of *Vardekloeftia* (Harris, 1932b), have ovulate heads that are surrounded by a "perianth" of numerous helically arranged bracts. This flower-like arrangement does not occur in any other group of gymnosperms and is thus interpreted as a relatively specialized feature within the Bennettitales.

6.6 "Corona." A "corona" occurs in *Williamsonia gigas, W. hildae, W. leckenbyi, Wielandiella angustifolia,* and the two species of *Williamsoniella, W. coronata* and *W. lignieri.* No comparable feature occurs in other gymnosperms, and I regard this as a specialization over the condition in other Bennettitales.

6.7 Bisporangiate (bisexual) "flowers." Bisporangiate "flowers" occur in *Cycadeoidea* and the two species of *Williamsoniella.* They are not known in other gymnosperms except the Gnetales (see character 1.7). They are interpreted here as a specialized feature within the Bennettitales, and the possibility that they are homologous with the "flowers" of the Gnetales is considered later in this paper (p. 775).

6.8 Microsporophylls laterally flattened. In those Bennettitales for which the microsporophylls are known, only in *Cycadeoidea, Williamsoniella coronata,* and *W. lignieri* are they laterally flattened. Dorsiventrally flattened leaf-like microsporophylls are generalized in seed plants, and the laterally compressed forms found in some Bennettitales are therefore interpreted as specialized.

6.9 Microsporophylls with three to four pairs of bivalved synangia. Both species of *Williamsoniella* have very similar microsporophylls, with three to four pairs of bivalved synangia. Other

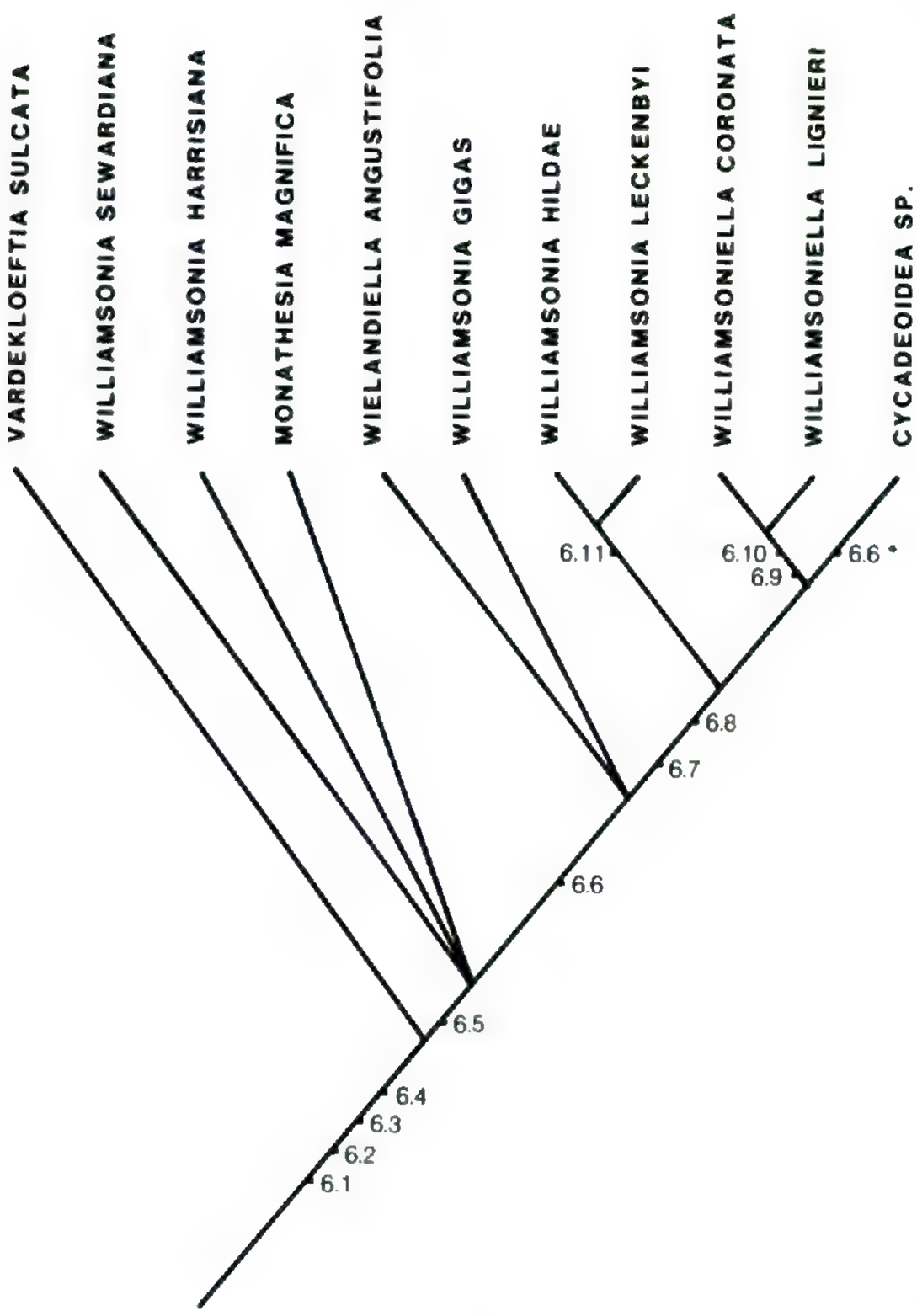


FIGURE 12. Preliminary cladogram summarizing relationships within the Bennettitales based on the data in Table 6. An asterisk indicates reversal of character 6.6. See text for further explanation.

gymnosperms generally have larger numbers of sporangia on each microsporophyll, and most other known bennettitalean microsporophylls have numerous synangia. The condition with few synangia is interpreted as a synapomorphy of *Williamsoniella* species.

6.10 Nilssoniopteris *leaves.* Both species of *Williamsoniella* have been linked with *Nilssoniopteris* leaves, and although recognized as two distinct species, *N. vittata* and *N. major* are very similar in morphology, venation, and cuticle (Harris, 1969: 75). Megaphyllous leaves in most seed plants, including most Bennettitales, are pinnate. In the context of the Bennettitales as a whole I therefore interpret *Nilssoniopteris* leaves as a synapomorphy of *Williamsoniella* species.

6.11 Synangia borne directly on the "rays" (microsporophylls). The microsporangiate "flowers" of *Williamsonia hildae* (*Weltrichia whitbiensis*) and *Williamsonia leckenbyi* (*Weltrichia pecten*) are extremely similar (Harris, 1969: 169), and differ from the microsporangiate flowers of *Williamsonia gigas* (*Weltrichia sol*) in having the synangia borne directly on the surface of the "rays" (microsporophylls) rather than on fertile lateral pinnae as in *Weltrichia whitbiensis, W. pecten, Williamsoniella,* and *Cycadeoidea.* The presence of these distinct fertile lateral pinnae is interpreted here as a primitive feature within the Bennettitales based on comparison with the pinnately divided microsporophylls of most "seed ferns."

DISCUSSION AND INTERPRETATION

The data matrix for the Bennettitales is given in Table 6 and the resulting cladogram in Figure 12. The Bennettitales have long been widely accepted as a natural group and at this level of analysis may be defined as monophyletic by the presence of interseminal scales, the characteristic cutinization of the guard-cells, the numerous ovules, and the bivalved synangia. The preliminary analysis presented here is the first attempt to clarify the interrelationships of the various taxa within the group. Although it provides some resolution, it is handicapped by lack of knowledge of microsporangiate organs in *Vardekloeftia, Williamsonia sewardiana, W. harrisiana, Wielandiella angustifolia,* and *Monanthesia.* In addition there is considerable diversity among Upper Triassic bennettitalean reproductive structures that needs to be incorporated into the analysis (Kräusel, 1948, 1949; Kräusel & Schaarschmidt, 1966). Several of these fossils (e.g., *Haitingeria krasseri, Leguminathus siliquosus, Leuthardtia ovalis, Westerheimia pramelreuthensis*) have unusual morphologies compared to the "flowers" of later Bennettitales and are currently being reinvestigated (Crane, work in progress).

It has been traditional to recognize two loosely defined families, the Cycadeoidaceae and Williamsoniaceae, within the Bennettitales (Stewart, 1983; Taylor, 1981a), but these do not form monophyletic groups in the cladogram. The Cycadeoidaceae are generally regarded as unified by having the flowers borne within an armor of persistent leaf bases and would include *Cycadeoidea* and *Monanthesia* considered in this analysis. The habit of these plants is similar but other characters do not place them together, and the flowers of *Williamsonia sewardiana* also are surrounded by at least some persistent leaf bases (Sahni, 1932b; see also Sharma, 1971). Unless other characters can be found to unite the Cycadeoidaceae, the two traditional families of Bennettitales have dubious phylogenetic utility. It should, however, be noted that the pattern of characters

TABLE 6. Data matrix for characters of Bennettitales.

Character	Other Seed Plants (excluding angiosperms)	*Vardekloeftia sulcata*	*Williamsonia sewardiana*	*Williamsonia harrisiana*	*Monanthesia magnifica*	*Wielandiella angustifolia*	*Williamsonia gigas*	*Williamsonia hildae*	*Williamsonia leckenbyi*	*Williamsoniella coronata*	*Williamsoniella lignieri*	*Cycadeoidea* sp.
6.1 Interseminal scales	–	+	+	+	+	+	+	+	+	+	+	+
6.2 Guard cells paracytic and heavily cutinized	–	+	+?	+?	+?	+	+	+	+	+	+	+?
6.3 Ovulate heads with numerous ovules	–	+	+	+	+	+	+	+	+	+	+	+
6.4 Bivalved synangia	–	+?	+?	+?	+?	+	+	+	+	+	+	+
6.5 "Perianth" of helically arranged bracts	–	–	+	+	+	+	+	+	+	+	+	+
6.6 "Corona"	–	–	–	–	–	+	+	+	+	+	+	–
6.7 Bisporangiate (bisexual) "flowers"	–	–	–	–	–	–	–	–	–	+	+	+
6.8 Microsporophylls laterally flattened	–	–?	–?	–?	–?	–?	–	–	–	+	+	+
6.9 Microsporophylls with 3–4 pairs of bivalved synangia	–	–?	–?	–?	–?	–?	–	–	–	+	+	–
6.10 *Nilssoniopteris* leaves	–	–	–	–?	–?	–	–	–	–	+	+	–
6.11 Synangia borne directly on the "rays"	–	–?	–?	–?	–?	–?	–	+	+	–	–	–

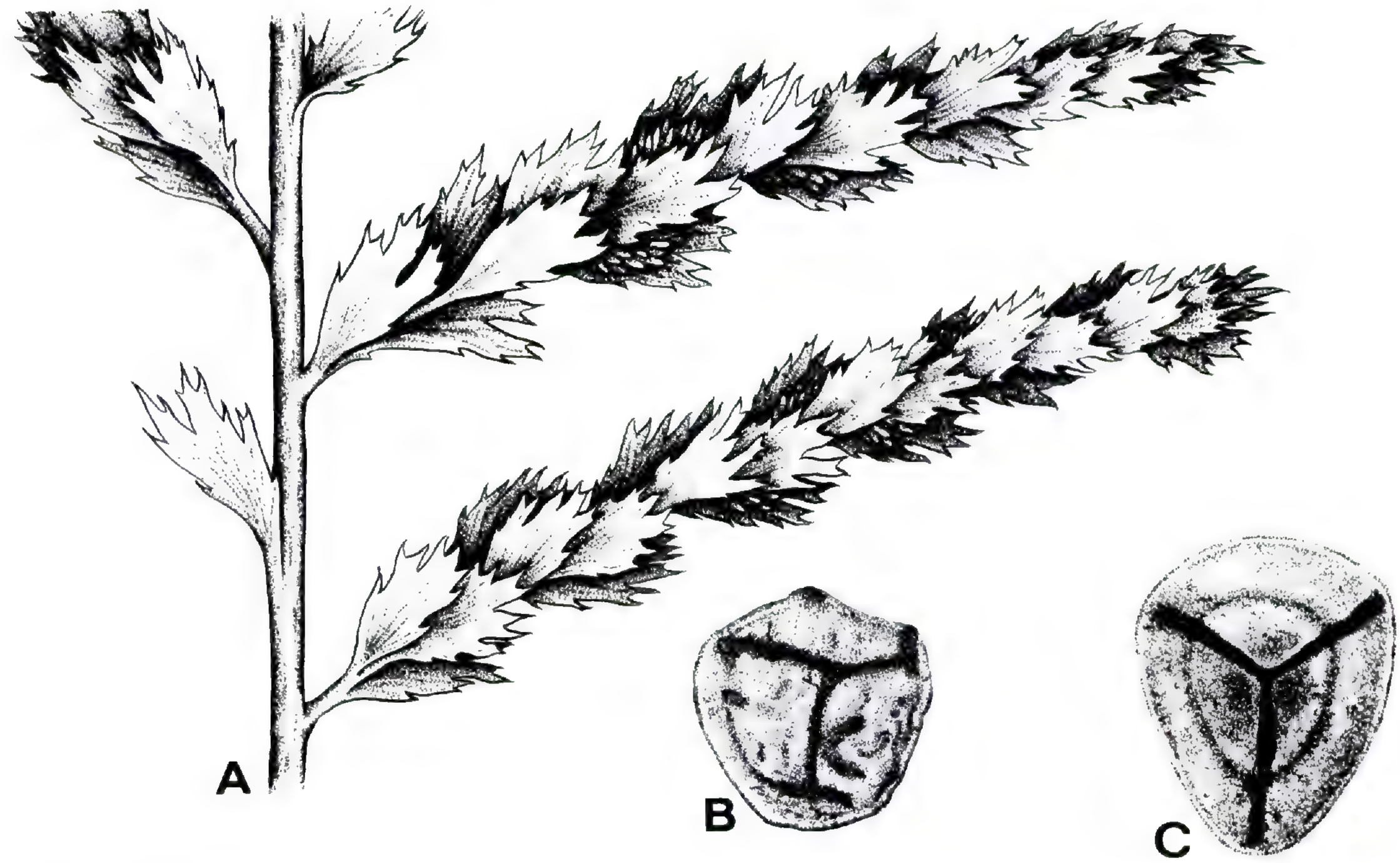


FIGURE 13. Morphology of *Archaeopteris*.—A. *A. macilenta,* fertile lateral branch systems based on Beck (1981, fig. 6.31) and Phillips et al. (1972, pl. 37, fig. 8); ca. ×1.5.—B. *Archaeopteris* sp. trilete microspore, based on Phillips et al. (1972, pl. 45, fig. 49); ×500.—C. *Archaeopteris* sp. trilete megaspore, based on Phillips et al. (1972, pl. 43, fig. 28); ×200.

accepted here suggests that the absence of the "corona" (character 6.6) from *Cycadeoidea* may be interpreted as secondary loss.

REPRESENTATIVE EXTANT AND FOSSIL GYMNOSPERMS

Having attempted to provide an outline of relationships within some groups of gymnosperms, the relationships between major seed plant taxa can be assessed. The principal constraint in such an analysis is the information available for many fossil seed plants. In this analysis I have attempted to keep assumptions concerning unknown characters to a minimum by using only the better understood fossil seed plants. This has excluded many potentially important fossil plants that need to be incorporated in future, more inclusive analyses. In this section I briefly review the characters of extant and fossil seed plants, emphasizing in particular the basis and limitations of our knowledge of fossil taxa.

ARCHAEOPTERIS

Archaeopteris (Fig. 13A) ranges from the mid-Devonian (Givetian) to Lower Mississippian (Tournaisian). It is an important Late Devonian plant and is the most completely understood of all progymnosperms (Beck, 1981; see Fig. 1). The plants were arborescent and eustelic with a large parenchymatous pith. There was a bifacial cambium that produced both secondary xylem and secondary phloem (Beck et al., 1982). The secondary xylem (*Callixylon*) was pycnoxylic and similar to that of extant conifers. The tracheids had uniseriate to multiseriate, circular, bordered pits on the radial walls (Beck, 1981: 202), and there was no axial parenchyma. The rays were uniseriate to multiseriate. *Callixylon* wood is known to have been attached to *Archaeopteris* branch systems (Beck, 1960, 1970). Although stem morphology and the pseudomonopodial branching of *Archaeopteris* is well understood, regular axillary branching does not occur (Beck, 1981: 212; Scheckler, 1978). Leaves were helically or decussately arranged and decurrent at the base (Fig. 13A), typically wedge-shaped, and varied from entire to deeply divided. The stomata of *Archaeopteris* have not been described.

Some lateral branch systems were fertile. The fertile leaves were generally deeply divided and bore microsporangia and/or megasporangia on their adaxial surface. Some species were heterosporous (Phillips et al., 1972), but whether other

species were homosporous or heterosporous is unknown. The microsporangia were long and slender, while megasporangia were shorter and broader. Both dehisced by a single longitudinal suture. The microspores (*Cyclogranisporites*) were about 40 μm in diameter, with a proximal trilete suture and a finely granular or smooth surface (Fig. 13B). The exine structure was granular (Pettitt, 1966). The megaspores (*Biharisporites*) were about 200 μm in diameter, with a trilete suture and a reticulate to rugulate surface (Fig. 13C; Phillips et al., 1972). Both microspores and megaspores presumably germinated proximally to produce free-living male gametophytes with motile spermatozoids and female gametophytes with well-developed archegonia. However, nothing is known of gametophyte development, gametes, or embryogenesis.

MEDULLOSANS

The medullosans are among the most extensively studied of all seed ferns (Stewart, 1983; Stidd, 1981a, 1981b). Typically, they have two or more vascular segments in the stem but this apparent "polystely" appears to be only a modification of the fundamentally eustelic arrangement in all other seed plants (Basinger et al., 1974; Beck et al., 1982). However, *Quaestora amplecta* (Mapes & Rothwell, 1980) from the Upper Mississippian of Arkansas, the earliest medullosan stem known, has an exarch protostele. If *Quaestora* is correctly interpreted as a medullosan it suggests that "polystely" may have arisen within the medullosan clade. The bifacial cambium produces secondary xylem and secondary phloem. The wood has multiseriate rays and is comprised of tracheids with multiseriate, oval, bordered pits on their radial walls. Despite extensive studies of medullosan anatomy (Stewart, 1983) and ontogeny (Delevoryas, 1955), axillary branching in medullosans has been demonstrated only once (Hamer, 1984 and pers. comm.). Medullosan leaves (e.g., *Alethopteris, Neuropteris, Odontopteris*) were large and pinnately organized, often with a bifurcated primary rachis. The petioles (*Myeloxylon*) contained a large number of scattered vascular bundles. Stomata have been described as paracytic (Oestry-Stidd & Stidd, 1976), but reinterpretation and better preserved material shows that they are anomocytic (Mickle & Rothwell, 1982; Reihman & Schabilion, 1978; Stidd, 1981a: 67).

Although a few specimens are known that show seeds apparently attached to medullosan foliage (Stewart, 1983: 260–261), most medullosan seeds, particularly those that are well understood anatomically (e.g., *Pachytesta illinoensis*), are linked with the vegetative parts on the basis of association evidence (Stewart, 1983: 260). The ovules (*Pachytesta, Trigonocarpus,* etc., see Hoskins & Cross, 1946; Taylor, 1965) are large (up to 11 cm long) and radiospermic. Each has a single integument with a sarcotesta, sclerotesta, and endotesta. The integument and nucellus are free except at the chalaza. Frequently the sclerotesta has three primary ribs, and often secondary and tertiary ribs also are developed. The ovules have a radially arranged double vascular system. The outer system has numerous traces that run within the sarcotesta between the ribs, while the inner system within the nucellus is formed by bundles or a network originating from a pad of vascular tissue at the chalazal end. The megaspore membrane in medullosan seeds is thick (5–25 μm) (Taylor, 1965).

Some medullosan pollen organs are large, complex synangiate structures with tubular sporangia that dehisce longitudinally (e.g., *Dolerotheca*), while others such as *Aulacotheca* and *Halletheca* are simpler, with fewer sporangia (Taylor, 1981b). Only a few of these pollen organs are known to have been attached to medullosan foliage (Dennis & Eggert, 1978), but convincing association and structural evidence has been presented for others (Ramanujam et al., 1974; Stewart, 1983). The majority of the pollen organs are known to have produced *Monoletes* (*Schopfipollenites*) pollen. These grains are large (100–500 μm long) and ellipsoidal. Distally there are often two longitudinal grooves and proximally a monolete suture with a marked deflection in the center. Occasionally (*Parasporites,* Dennis & Eggert, 1978) the grains have a pair of small sacci. The pollen wall is alveolar, with numerous fine cavities (Taylor, 1978). Pollen wall ultrastructure is similar to that of cycads, but the ontogeny is apparently different (Taylor, 1982; Taylor & Rothwell, 1982), and the wall cavities are much less regular. Germination is thought to have been proximal (prepollen sensu Chaloner, 1970a); male gametes were probably motile. *Monoletes* pollen has been described in the pollen chamber of *Pachytesta hexangulata* (Stewart, 1951). Little is known of male gametophyte development, but the pollen contents figured by Stewart (1951) are suggestive of the spermatozoids of extant cycads and hence zooidogamy.

The details of female gametophyte development are unknown in medullosans, but the gametophyte is cellular, with archegonia at fertilization (Stewart, 1951). Nothing is known of embryogenesis, and an embryo has never been described from a medullosan seed (Stewart, 1983: 282–283).

CYCADS

Possible defining characters of cycads have already been discussed (Fig. 5). The primary vascular architecture of extant cycads is not understood clearly (Beck et al., 1982), but evidence from microsporangiate cones suggests that the vasculature is fundamentally eustelic (Beck et al., 1982: 755). Typically the stem has a large pith, and the bifacial cambium (or cambia in *Encephalartos* and *Macrozamia,* Sporne, 1971a: 108) produces relatively small amounts of secondary xylem and phloem. The secondary xylem consists of tracheids with multiseriate bordered pits and has many rays. In *Zamia* and *Stangeria* the wood has tracheids with scalariform pitting (Sporne, 1971a: 108). The growth of most cycad stems is sympodial (see character 2.2), and some genera (e.g., *Stangeria* and *Bowenia*) are irregularly branched. According to Bierhorst (1971: 373), Stopes (1910), and Stevenson (1980) branching is adventitious, and Foster and Gifford (1974: 419) observed that some lateral buds form from the living tissues of persistent leaf bases while others arise due to injury. There are no detailed developmental studies of branching in cycads. Cycad leaves are generally large and pinnate with dichotomous venation, although some anastomoses do occur (Foster & Gifford, 1974: 422–423). The stomata are anomocytic.

The ovules are borne on simple megasporophylls that are generally arranged in cones (see character 2.2). There are generally two ovules per megasporophyll, although some species of *Cycas* may have up to eight. The ovules are large (up to 6 cm long, Chamberlain, 1935: 104) and radially symmetrical. Each has a single massive integument with three layers: a fleshy sarcotesta, a hard sclerotesta, and an endotesta. The integument and nucellus are "fused" except close to the micropyle. The ovule is supplied by a double, radially arranged, vascular system. There are about ten vascular bundles that run up the outside of the sclerotesta, and an inner anastomosing system of vascular bundles that run in the endotesta to the level at which the integument and nucellus are free. The megaspore membrane is well developed and may be up to 10 μm thick in mature ovules (Chamberlain, 1935: 126; Erdtman, 1965), but the nucellus and inner lining of the integument is only weakly cutinized (Harris, 1954).

The microsporophylls of all cycads are borne in cones and bear microsporangia on their abaxial surface. In *Cycas* there may be more than 1,000 microsporangia, but in *Zamia* there are 25 or less (Chamberlain, 1935: 115). The microsporangia are arranged in sorus-like clusters of two to six, each supplied by a single vein (Stevenson, 1982). Each microsporangium dehisces by a single slit towards the center of the "sorus." The pollen is boat-shaped, non-saccate, and more or less smooth-walled. The pollen wall is alveolate with numerous fine cavities (Audran & Masure, 1977). The male gametophyte is generally five-celled (see character 1.1), and the final division of the spermatogenous cell produces two large spermatozoids up to 400 μm in length (Norstog, 1977) with a spiral band of flagella (Sporne, 1971a: 116). The pollen germinates distally, producing a haustorial pollen tube, and the spermatozoids are released by a rupture in the pollen tube close to the distal pollen wall.

The female gametophyte develops from a single functional megaspore (see character 1.2) that undergoes free nuclear divisions until over 1,000 nuclei have been produced, before centripetal cellularization (Sporne, 1971a: 114) and the formation of archegonia. Following fertilization, free nuclear division produces 64–1,000 nuclei before cellularization occurs (Sporne, 1971a: 116).

LYGINOPTERIS

Lyginopteris oldhamia is known from the Upper Carboniferous (Westphalian A) of Europe (Oliver & Scott, 1904; Stewart, 1983). The name is applied to small stems, up to 4 cm in diameter (Taylor & Millay, 1981: 38), of possibly vine-like habit (Stewart, 1983; Taylor & Millay, 1981). The primary vasculature was eustelic (Beck et al., 1982; Scott, 1923), and a bifacial cambium produced relatively little secondary xylem and phloem. The wood contained large tracheids with multiseriate, oval bordered pits on the radial walls. The rays were wide and multiseriate. Regular axillary branching occurred. Leaves were widely separated and borne helically on the stem. They were small, pinnately organized, and highly dissected. The primary rachis bifurcated shortly

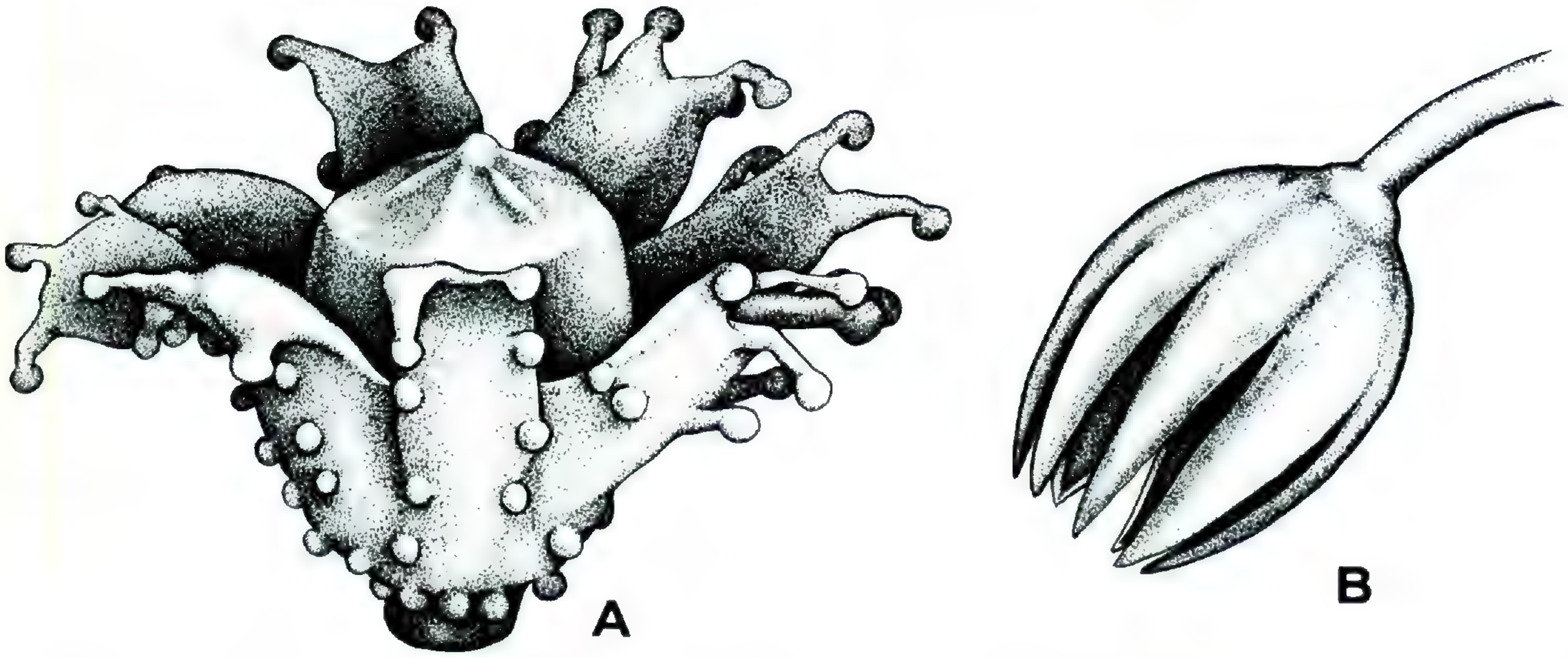


FIGURE 14. Morphology of *Lagenostoma* and *Telangium*.—A. *L. lomaxii*, cupule and ovule, based on Oliver and Scott (1904, text-fig. 2); ×5.—B. *T. scottii*, pollen organ, based on Benson (1904, figs. 1, 9, 10); ×7.5.

after leaving the stem. On the basis of association and the occurrence of large, distinctive, stalked, capitate glands, *Sphenopteris hoeninghausii* (*Rachiopteris aspera* when anatomically preserved) is thought to be the foliage of *L. oldhamia*.

The ovules of *Lyginopteris* (*Lagenostoma lomaxii*, Fig. 14A) are known attached to *Sphenopteris hoeninghausii* foliage. They were borne terminally on the distal part of the fronds in pedicellate cupules. Each cupule contained a single ovule. The upper half of the cupule bore eight to ten distal lobes, each supplied by a single vascular strand. The ovules were small (about 5.5 mm long) and radiospermic. The single integument was "fused" with the nucellus except near the micropyle. The integument was supplied by eight or nine radially arranged bundles in the endotesta. The megaspore membrane was thick (Oliver & Scott, 1904) and may be up to 5 μm in some lyginopterid pteridosperms (Taylor & Millay, 1981). It is unknown whether the megaspore of *L. lomaxi* had a trilete mark, but this feature does occur in other lyginopterid megaspores (Pettitt, 1969; Schabilion & Brotzman, 1979), and in *Stamnostoma huttonense* there is a cluster of three aborted spores at the apex of the megaspore (Long, 1975). This suggests that lyginopterid megaspores were derived from a tetrahedral rather than linear tetrad.

The microsporangiate organs of *Lyginopteris* are frequently considered to be *Crossotheca* (Kidston, 1906; Sporne, 1971a: 55), but there is no evidence linking these two organs as part of the same plant (Jongmans, 1930). *Lyginopteris oldhamia* and *Lagenostoma lomaxii* come from strata older (Westphalian A) than those in which *Crossotheca* is typically abundant. Benson (1904) made a good case for *Telangium scottii* (Fig. 14B) being the *Lyginopteris* microsporangiate organ, based on anatomical similarity and association evidence. *Telangium scottii* comprises bilaterally symmetrical synangia with six to eight ellipsoidal sporangia that dehisced along their inner wall. The pollen (prepollen) was small with a proximal trilete mark. The pollen wall ultrastructure is unknown, but in other supposed lyginopterids (e.g., *Crossotheca*, Millay et al., 1978) it is structurally homogeneous. Male gametophyte development is unknown, but presumably germination was proximal and produced motile sperm. The large flagellate spermatozoids described in the micropyle of *Lagenostoma ovoides* (Benson, 1908) would be worth reexamining.

The female gametophyte of *Lagenostoma lomaxii* was cellular, and the development probably involved an initial free nuclear phase followed by centripetal cellularization (McLean, 1912; Oliver & Scott, 1904). The female gametophytes of *L. ovoides* and *Hydrasperma tenuis* were also cellular, and archegonia have been described (Long, 1944; Matten et al., 1984). Long (1975) has described a possible lyginopterid embryo from the Lower Carboniferous of Scotland, but embryos of *Lagenostoma* and all lyginopterid pteridosperms are otherwise unknown.

CORDAIXYLON

Several species of microsporangiate and ovulate *Cordaianthus* inflorescences have been de-

scribed in the literature (Rothwell, 1977; Daghlian & Taylor, 1979), but only one is known as part of a "whole plant" (Rothwell & Warner, 1982, 1984). The description given here is based on the *Cordaianthus* inflorescences attached to *Cordaixylon dumusum* stems and leaves from the Late Pennsylvanian of eastern Ohio (Rothwell & Warner, 1982, 1984).

The mature stems were up to about 5 cm in diameter and produced abundant adventitious roots. The plant is reconstructed as a small shrub. The primary vascular system was an endarch eustele, and a bifacial cambium produced secondary xylem and secondary phloem. The secondary xylem was composed of tracheids with crowded multiseriate oval bordered pits on the radial walls. The rays were predominantly uniseriate. Leaves were helically arranged and ranged from needle-like with a single vein to spatulate forms up to 3 cm wide with numerous veins. Some branches bore needle-like leaves at the base and spatulate leaves distally. Others bore needle-like leaves throughout. Anatomical details of the leaves are described by Rothwell and Warner (1984). The stomata consisted of two guard cells with two lateral and two subsidiary cells.

Inflorescences were borne irregularly as epicormic branches on the stems. Frequently the xylem of the cone axis was not continuous with the xylem of the stem. Ovulate inflorescences (*Cordaianthus duquesnensis* Rothwell, 1982b) consisted of a bilaterally symmetrical primary axis bearing four rows of fertile secondary shoots, each in the axil of a bract. The secondary shoots had 60–70 helically arranged scales of which the distal 20–30 were fertile and bore a single terminal ovule. Immature ovules are known attached to the inflorescence and are linked by a continuous morphological series with mature ovules of *Cardiocarpus oviformis* Leisman (1961) that occur in the same deposit. These mature ovules were up to about 9 mm long and distinctly flattened. There was a single integument that was free from the nucellus except at the chalaza. Each ovule was supplied by a single vascular bundle that expanded to form a flattened plate at the base of the nucellus. Below this plate the main vascular bundle produced two lateral traces that ran through the sarcotesta in the primary plane, one on either side of the nucellus. The megaspore membrane was about 5 μm thick.

The structure of the microsporangiate inflorescence was similar to that of the ovulate inflorescences, consisting of a bilaterally symmetrical primary axis with four rows of fertile secondary shoots, each in the axil of a bract. The secondary shoots bore helically arranged scales the distalmost of which were fertile. Each fertile scale bore five microsporangia arranged in a ring at the apex. The microsporangia were fused proximally and free distally. Pollen was saccate and of the *Florinites* type. *Florinites* pollen has a distal thinning of the wall and an alveolate wall structure with large cavities.

Nothing is known of cordaite male gametophytes from North American material, but Florin (1936) described male gametophytes from *Florinites* in situ within *Cordaianthus* from Europe (Millay & Eggert, 1974). Florin's material shows axial rows of four or five cells in each grain, and the male gametophyte was therefore basically similar to that seen in many conifers and *Ephedra* (Millay & Eggert, 1974; Fig. 2, see character 1.1). Germination was probably distal (Millay & Taylor, 1974). The female gametophyte of *Cardiocarpus oviformis* was cellular and possessed two archegonia as described in *C. spinatus* by Andrews and Felix (1952). Nothing is known of the embryo of the "*Cordaixylon* plant."

MESOXYLON

The cordaite inflorescence *Gothania* was described originally from European material (Scott, 1919), but knowledge of the *Gothania* plant has been increased considerably by description of *G. lesliana* from the Middle Pennsylvanian of Kentucky (Daghlian & Taylor, 1979) and *Mesoxylon priapi* from the Upper Pennsylvanian of eastern Ohio (Trivett, 1983; Trivett & Rothwell, 1985). On the basis of association in both European and North American coal balls, Daghlian and Taylor (1979) suggest that *G. lesliana* is the microsporangiate fructification of a *M. sutcliffi* stem with *Cordaites felicis* foliage and *Mitrospermum compressum* ovules. Trivett and Rothwell (1985) describe *Mesoxylon priapi* based on stems with attached *Cordaites felicis* foliage and microsporangiate inflorescences of the *Gothania* type. This material forms the basis for the description given here.

Mesoxylon stems (Beck et al., 1982; Scott & Maslen, 1910) had a primary vascular system consisting of a modified mesarch eustele. A bifacial cambium produced secondary xylem and secondary phloem. The secondary xylem was composed of tracheids with crowded multise-

riate oval bordered pits on the radial walls. The rays were two to four cells wide. Axillary branching is known to occur and axillary buds were covered with needle-like bud scales. The leaves (*Cordaites felicis*) were helically arranged, probably spatulate, and several centimeters wide with numerous veins. Anatomical details of the leaves are described by Benson (1912), Good and Taylor (1970), and Trivett and Rothwell (1985). The stomata consisted of two guard cells with two lateral and two subsidiary cells.

Inflorescences were borne in the axils of leaves. Occasionally both an inflorescence and a vegetative bud occur in the axil of a single leaf. Ovulate inflorescences are unknown, but were presumably similar to those of *Cordaixylon dumusum,* consisting of a bilaterally symmetrical primary axis bearing four rows of fertile secondary shoots, each in the axil of a bract. Mature ovules of *Mitrospermum vinculum* (Grove & Rothwell, 1980) occur in the same deposit as *M. priapi* and contain abundant pollen from the *Mesoxylon* plant in the micropyle. Mature ovules were up to about 4 mm long and distinctly flattened. There was a single integument that was free from the nucellus except at the chalaza. The ovule was supplied by a single vascular bundle that expanded to form a flattened plate at the base of the nucellus. Below this the main vascular bundle produced two lateral traces that passed through the sclerotesta and extended to the micropyle in the sarcotesta. The bundles were positioned one on either side of the nucellus in the primary plane of the ovule. The megaspore membrane was 6–13 μm thick.

The structure of microsporangiate inflorescence was similar to that of the ovulate inflorescences, consisting of a bilaterally symmetrical primary axis with four rows of fertile secondary shoots. The secondary shoots had up to 28 helically arranged scales. There were about five fertile scales confined to the distal part of the shoot and each bore four microsporangia arranged in a row at the apex. The microsporangia were free throughout their length. Pollen was saccate and of the *Sullisaccites* type. *Sullisaccites* has a distal monolete or trilete suture and an alveolate wall structure with large cavities (Millay & Taylor, 1974). *Gothania lesliana* produced monosaccate *Felixipollenites* pollen with a monolete or trilete proximal suture. The pollen wall was alveolate, with irregular, medium-sized cavities (Taylor & Daghlian, 1980). Nothing is known of male gametophyte development, but both *Felixipollenites* and *Sullisaccites* (prepollen) are thought to have germinated proximally.

Nothing is known of the female gametophyte or embryo of *Mesoxylon.* Male and female gametophytes of other cordaites are known and discussed under *Cordaianthus.*

CONIFERS

Possible defining characters of conifers have been discussed already (Fig. 6). The primary vasculature of the stem is eustelic (Beck et al., 1982) with a single bifacial cambium producing secondary xylem and phloem. The secondary xylem is pycnoxylic, characteristically with uniseriate rays, and the tracheids have uniseriate to multiseriate circular bordered pits, generally confined to the radial walls. Some genera have long- and short-shoot systems, and axillary branching occurs. Although there is considerable variation in leaf morphology (see character 3.1), no conifer has pinnate leaves. Stomata are anomocytic (but see Scott & Chaloner, 1983).

Ovulate cones are diverse in form, but all are regarded as fundamentally compound, with cone scales interpreted as fertile shoots in the axils of bracts (see character 3.3). The ovules vary considerably in size and are flattened. Each has a single integument, which frequently has two "horns" on either side of the micropyle in the primary plane (Bierhorst, 1971, figs. 25.3B, 25.3C, 25.5E). These "horns" reflect the ontogenetic development from two opposite primordia that also are positioned in the primary plane (Bierhorst, 1971, fig. 25.5C, 25.5D; Florin, 1951: 364). The integument and nucellus may be "fused" for most of their length or free except at the chalaza. The ovule lacks a well-developed vascular system, and frequently there are no bundles at all (Chamberlain, 1935: 298). The megaspore membrane varies in thickness and complexity of structure. In the Pinaceae and Podocarpaceae it may be 4–6 μm thick, whereas in the Araucariaceae, Cupressaceae, Cephalotaxaceae, Taxaceae, and Taxodiaceae it is generally less well developed and may be extremely thin (Erdtman, 1965). It is also thick in *Lebachia* (Mapes & Rothwell, 1984, pl. 15, fig. 2). Outgroup comparison with cycads, *Ginkgo,* and pteridophytes suggests that the thick megaspore membrane is the primitive condition in the conifers, thinner membranes being more specialized. The nucellus and inner lining of the integ-

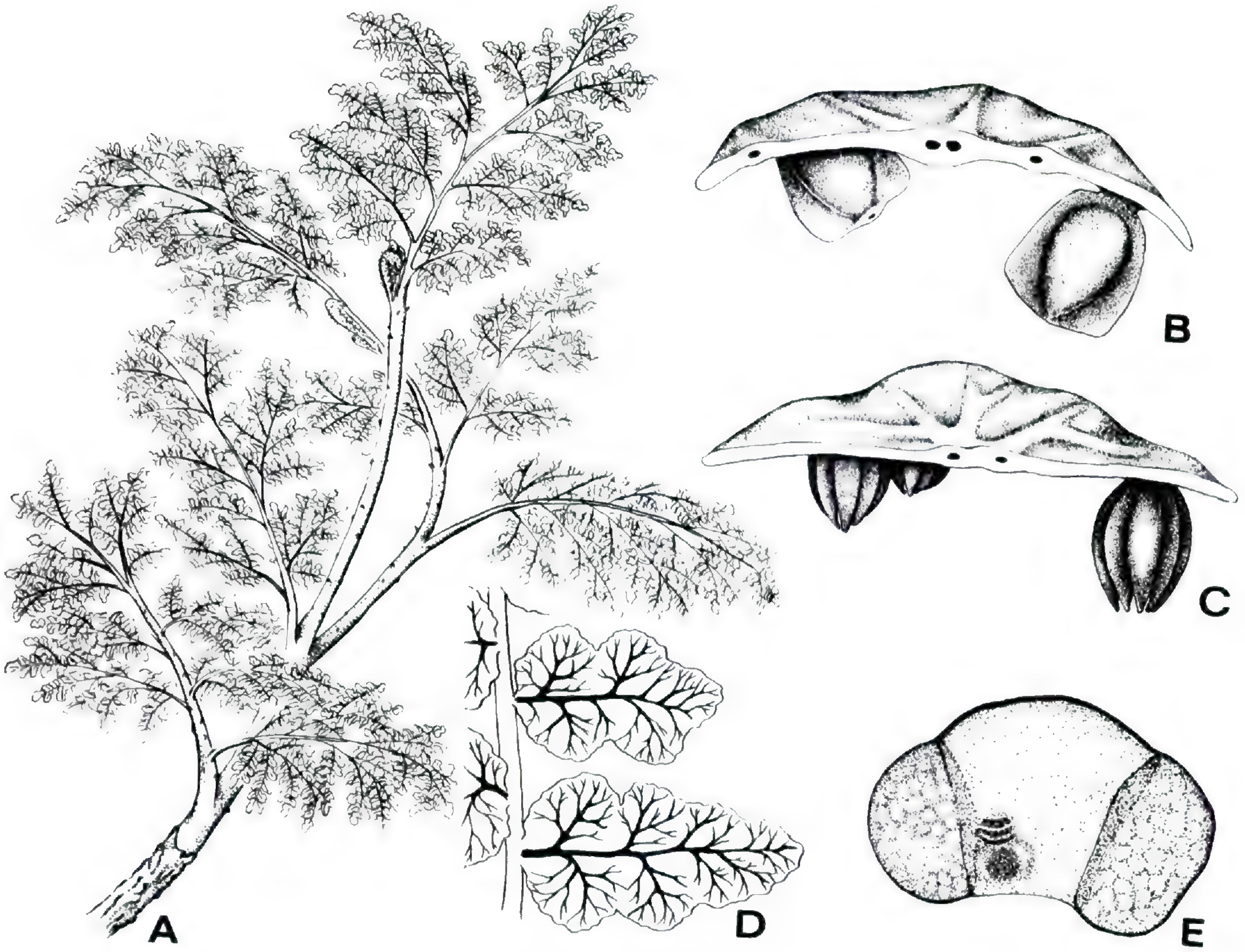


FIGURE 15. Morphology of the *Callistophyton* plant.—A. *Callistophyton,* branch system, redrawn from Rothwell (1975, text-fig. 1); ×0.25.—B. *Callospermarion pusillum,* fertile pinnule segment bearing two abaxial ovules, based on Rothwell (1981, fig. 3), note that details of seed attachment in *Callistophyton* are not well understood, see text; ×5.—C. *Callistophyton,* pinnule bearing three adaxial microsporangiate synangia, based on Rothwell (1981, fig. 3A); ×10.—D. *C. boyssetii* detail of proximal pinnules, based on Rothwell (1981, fig. 2B); ×2.5.—E. *Vesicaspora* pollen grain from an *Idanothekion glandulosum* pollen sac showing microgametophyte, based on Rothwell (1981, pl. 3, fig. 7); ×900.

ument are generally only weakly cutinized (Harris, 1954).

The microsporangiate cones of conifers are extremely variable, but they are all usually considered to be fundamentally simple structures with microsporophylls bearing abaxial microsporangia. There are several kinds of pollen (Erdtman, 1965; Wodehouse, 1935), but saccate grains with a distal aperture are interpreted here as primitive for extant conifers based on out-group comparison with *Lebachia* (see Fig. 6). Saccate pollen is accepted here as primitive for the group. The pollen wall structure in most saccate grains is alveolate with large cavities, but in the non-saccate conifers (e.g., Araucariaceae, Cupressaceae) the pollen wall is granular (Doyle et al., 1975).

Male gametophyte development varies (Sporne, 1971a: 142), but the developmental pattern that occurs in cycads, *Ginkgo,* and *Ephedra* is accepted here as primitive for the group (see character 1.1). The pollen germinates distally and fertilization is typically siphonogamous, although there are rare reports of zooidogamy in conifers (Christiansen, 1969).

The female gametophyte develops from a single functional megaspore (see character 1.2) that undergoes free nuclear divisions before centripetal cellularization occurs and archegonia are formed. Following fertilization there is a very short free nuclear phase in the development of the embryo.

GINKGO

The genus *Ginkgo* contains a single extant species, *G. biloba,* although there are several fossil species, mostly known from foliage only (Tralau, 1968). The primary vasculature of the stem

is eustelic (Beck et al., 1982) with a single bifacial cambium producing secondary xylem and phloem. In long shoots the secondary xylem is pycnoxylic and conifer-like with narrow rays, and uniseriate or biseriate circular bordered pits on the radial walls of the tracheids. Short shoots have manoxylic wood. Axillary branching occurs. The distinctive fan-shaped leaves have two vascular bundles in the petiole. The venation is dichotomous with a few anastomoses (Foster & Gifford, 1974: 449). Stomata are anomocytic.

The ovules are borne in pairs at the end of stalks in leaf axils. The stalks are slightly dorsiventrally flattened and contain two pairs of vascular bundles. Each ovule bearing stalk is interpreted as a short shoot bearing two uniovulate fused megasporophylls each represented by a pair of vascular bundles (Rothwell, pers. comm.). The ovules are large (up to 4 cm long) and either flattened or trigonous. Each has a single, massive integument that frequently has two apical "horns," one on either side of the micropyle in the primary plane (Bierhorst, 1971: 421, fig. 24-4B). There is a sarcotesta, a sclerotesta, and endotesta. The integument and nucellus are "fused" except close to the micropyle. The ovule is supplied by two (or three) poorly developed vascular strands that run inside the sclerotesta to the level at which the integument and nucellus are free. The vascular bundles run in the primary plane, and the sclerotesta has two (or three) distinct ribs. Occasional ovules may have three or four vascular bundles and a corresponding number of ribs. The megaspore membrane is well developed and up to 4–6 μm thick at maturity (Chamberlain, 1935: 208; Erdtman, 1965: 10, but see *Karkenia,* Archangelsky, 1965); the nucellus and inner lining of the integument are only weakly cutinized (Harris, 1954).

The microsporangiate organs also arise in the axils of leaves and consist of a lax inflorescence bearing numerous lateral stalks interpreted here as microsporophylls. Each microsporophyll bears a pair of pendant microsporangia and an apical mucilage-containing "knob" (Sporne, 1971a: 169). At the base of each lateral stalk there is a pair of minute projections. The sporangia dehisce by a single longitudinal slit. The pollen is boat-shaped, non-saccate, and more or less smooth-walled. The pollen wall is alveolate, with large cavities similar to those in many conifers (Zavada & Crepet, pers. comm.). Male gametophyte development is similar to that in *Ephedra* and some conifers (character 1.1). As in cycads, the final division of the spermatogenous cell produces two large spermatozoids with a spiral band of flagellae (Sporne, 1971a: 170). The pollen germinates distally, produces a haustorial pollen tube, and the motile spermatozoids are released by a rupture in the pollen tube close to the distal pollen wall.

The female gametophyte develops from a single functional megaspore (see character 1.2), which undergoes free nuclear divisions until about 256 nuclei are formed, before cellularization occurs centripetally and archegonia are formed (Sporne, 1971a: 169). Following fertilization, free nuclear divisions produce 256 nuclei before cellularization of the embryo occurs (Chamberlain, 1935: 211; Sporne, 1971a: 171).

CALLISTOPHYTON

Callistophyton (Fig. 15) is currently the best understood of all seed ferns based on Middle and Upper Pennsylvanian material from North America. Its morphology and reproductive biology are reviewed by Rothwell (1975, 1980, 1981). Stems of *Callistophyton* are up to 3 cm in diameter, and the plant is thought to have been small and shrubby with a scrambling habit (Fig. 15A). The primary vasculature of the stem is eustelic with a pith and a ring of five sympodia, as is typical of *Lyginopteris* and many fossil conifers. The secondary xylem is well developed, typically with biseriate rays but with some up to five cells thick. Tracheids have alternate multiseriate oval bordered pits on the radial walls. The secondary phloem produced by the bifacial cambium consists of radial files of sieve cells and phloem parenchyma with scattered rays. The stem and all other parts of the plant contained spherical secretory cavities, each lined with an epithelium. Adventitious roots were formed at many of the nodes, and axillary branching occurred. The axillary buds were covered by small linear scales. The leaves (Fig. 15D) were very variable in size, and bi-, tri-, or quadripinnate. They were helically arranged on the stem. The stomata have not been described.

The ovules (*Callospermarion*) were borne scattered on the abaxial surface of the leaves (Fig. 15B). Each was flattened with two planes of symmetry. There was a single integument that was free from the nucellus except at the chalaza. It was vascularized by two vascular bundles in the primary plane of the sarcotesta. At the base of

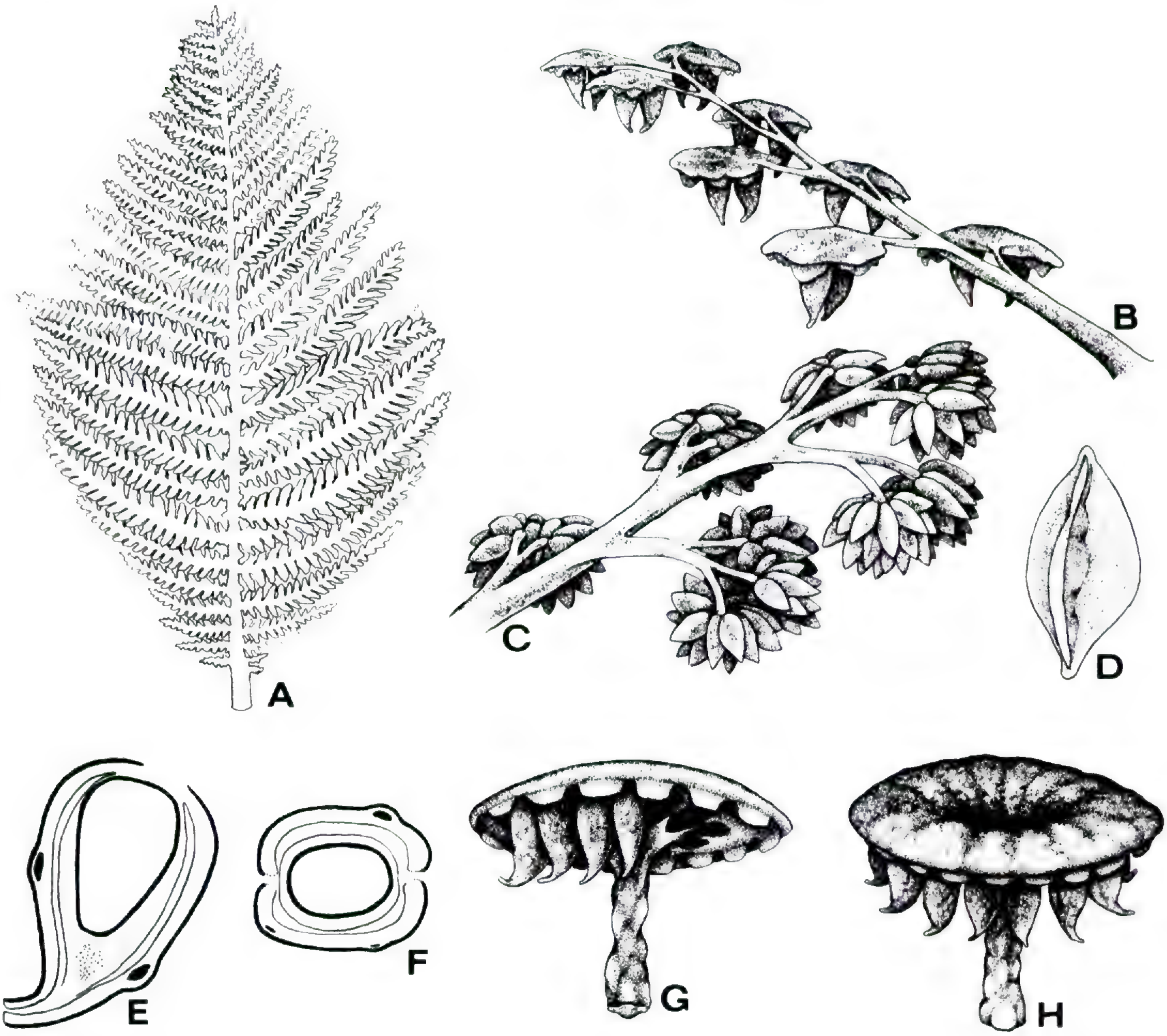


FIGURE 16. Morphology of peltasperms.—A. *Lepidopteris stormbergensis,* bipinnate frond, based on Thomas (1933, fig. 53); ×0.25.—B. *Autunia thomasii,* megasporophyll based on Townrow (1960, text-figs. 10B, 11); ×3.—C. *Antevsia zeilleri,* based on Harris (1932a, pl. 7, fig. 1); ×2.—D. Pollen of *A. zeilleri,* redrawn from Townrow (1960, text-fig. 7J); ×750.—E. *Peltaspermum rotula,* longitudinal section of ovule, redrawn from Harris (1932a, fig. 28E); ×4.—F. *P. rotula,* transverse section of ovule, redrawn from Harris (1932a, fig. 28E); ×4.—G. *P. rotula,* peltate organ bearing a circle of ovules on the lower surface, most ovules removed for clarity, based on Harris (1932a, fig. 28I); ×1.5.—H. *P. rotula,* peltate organ bearing ovules on the lower surface, based on Harris (1932a, fig. 28I, pl. 8, fig. 1); ×3.

the nucellus there was a distinct disc of vascular tissue. The megaspore membrane was up to 10 μm thick (Rothwell, 1971).

The microsporangiate organs (*Idanothekion*) were radially symmetrical synangia borne abaxially on pinnules (Fig. 15C). Each consisted of six to eight sporangia united for half their length. Distally they formed a tube and dehisced towards the center along a single median suture. The sporangia produced monosaccate pollen of the *Vesicaspora*-type with a distal sulcus (Fig. 15E). The pollen wall is alveolate, similar to that of conifers.

Pollen occurs frequently in the micropyles of *Callospermarion* ovules, and a slender, branched pollen tube similar to that of extant conifers has been described (Rothwell, 1972). Germination was distal, and the tube is unlike the larger inflated haustorial structures of extant cycads and *Ginkgo* (Rothwell, 1980: 92). It seems likely that the *Callistophyton* pollen tube indicates siphonogamy. *Vesicaspora* pollen has been described with cellular contents preserved, and the four-celled axial row has been interpreted as three prothallial cells with a larger antheridial cell (Rothwell, 1981: 114). Microgametophyte development was

TABLE 7. Isolated organs of the three better understood peltasperms (after Townrow, 1960; Kerp, 1982).

Locality	Leaf	Megasporophyll	Microsporophyll
South Africa (M. Triassic)	*Lepidopteris stormbergensis*	*Autunia thomasii*	*Antevsia extans*
Sweden & E Greenland (U. Triassic)	*Lepidopteris ottonis*	*Peltaspermum rotula*	*Antevsia zeilleri*
Nahe, West Germany (L. Permian)	*Callipteris conferta*	*Autunia milleryensis*	—

therefore basically similar to that in *Ephedra,* some conifers, and cordaites (*Florinites,* Millay & Eggert, 1974; see character 1.1).

Megagametophyte development is thought to have involved free nuclear divisions, followed by centripetal cellularization and differentiation of two archegonia. Cellular embryos have not been recognized.

PELTASPERMS

The Peltaspermaceae range from the Lower Permian to Upper Triassic and are known from leaves (*Callipteris conferta, Lepidopteris*), microsporophylls (*Antevsia*), and megasporophylls (*Autunia, Peltaspermum*) (Fig. 16) (Antevs, 1914; Harris, 1932a, 1937; Kerp, 1982; Lundblad, 1950; Mamay, 1975, 1978; Salmenova, 1979; Thomas, 1933; Townrow, 1960). Two species are known from all three organs (Table 7). The individual organs never have been found connected, but they all show highly characteristic blister-like swellings of the cuticle. This and other cuticular similarities, combined with association, provide evidence to link them together.

Almost nothing is known of the stem of the peltasperms (Townrow, 1960: 340), but the leaves apparently were deciduous, and this suggests that the plants were woody. The leaves were bipinnate (Fig. 16A) with bulbous frond bases. Pinnules were borne both on the pinnae and directly on the leaf rachis. Stomata were anomocytic.

Four species of megasporophylls have been described (Kerp, 1982): *Autunia dzungaricum* (*Peltaspermum dzungaricum* Salmenova, 1979); *A. milleryensis*; *A. thomasii* (*P. thomasii,* Harris, 1937; Thomas, 1933; Townrow, 1960); and *P. rotula* (Harris, 1932a). They were dorsiventrally organized and branched in a single plane (Townrow, 1960). It is not known how they were attached to the plant. Each lateral "branch" (interpreted here as a pinna of the megasporophyll) terminated in a swollen lamina that bore seeds on the lower surface. In *A. dzungaricum, A. milleryensis,* and *A. thomasii* the lamina bore two seeds lateral to the insertion of the "branch" (Fig. 16B). In *P. rotula* the seed bearing lamina was peltate with the "branch" inserted centrally to the undersurface: ten to 12 seeds were arranged around the insertion of the "branch" (Fig. 16G, H). The lobed margin of the lamina in *P. rotula* was reflexed and attached to the "branch." Only the ovules of *P. rotula* are known in detail (Fig. 16E, F). They were flattened and unitegmic with a long, bilobed, micropylar tube. The cuticle of the outer integument separated into two halves on maceration (Harris, 1932a: 69), and I interpret this as reflecting a platyspermic organization of the seed. Nothing is known of seed vasculature. The nucellus was free from the integument except at the base. The megaspore membrane was thick and resistant to maceration.

Microsporophylls (*Antevsia*) were bipinnate, with alternate primary branching in one plane (Fig. 16C). It is not known how they were attached to the plant. Secondary branching was irregular and frequently at 90° to that of the primary branching. Secondary branches were short and bore four to 12 unilocular, pendulous pollen sacs that dehisced along a single longitudinal suture. Pollen was ellipsoidal, non-saccate, with a single distal sulcus (Fig. 16D). Fine structure of the pollen wall is unknown.

Nothing is known of the gametophytes or embryo of peltasperms.

GLOSSOPTERIDS

An outline cladogram of glossopterids has been presented already (Fig. 8); only additional features thought to be general for the group are mentioned here.

The *Glossopteris* plant is thought to have been a large tree (Gould & Delevoryas, 1977; Pant, 1977a). The primary vasculature was eustelic, and a bifacial cambium produced secondary phloem and large amounts of secondary wood (*Araucarioxylon*). The wood was pycnoxylic, with

tracheids with multiseriate opposite or alternate circular bordered pits. The rays were uniseriate. Secondary xylem of identical structure is known to have been produced in the roots (*Vertebraria,* Gould, 1975). Axillary branching is known to have occurred. The leaves were borne in whorls or spirals, probably on long and short shoots (Pant, 1977a). The leaves were simple and narrowly elliptical with a midrib and well-developed reticulate venation (character 4.1). Stomata were anomocytic.

The ovules were borne on different kinds of megasporophylls (see characters 4.2, 4.5) in the axil of a leaf. The ovules of the silicified Australian material (Gould & Delevoryas, 1977) were not described in detail, but they appear to have been pyriform, and some appear flattened (Gould & Delevoryas, 1977, fig. 7c). Those associated with permineralized Antarctic *Glossopteris* material (Schopf, 1976: 56–57) were distinctly platyspermic, and the vasculature was probably "similar to cordaitean ovules" (Schopf, 1976: 57). The *Glossopteris* ovules described from compressions (e.g., *Pterygospermum,* Pant & Nautiyal, 1960) also were flattened, with a single integument and a long micropylar tube. The integument and nucellus were apparently free except at the chalaza. The nucellar cuticle was robust, but a megaspore membrane up to 6 μm thick also was present (Pant & Nautiyal, 1960).

The microsporophylls were borne adnate to a *Glossopteris* leaf (character 4.3). The sporangia (*Arberiella*) had a finely striated wall and dehisced by a single longitudinal slit. They produced saccate pollen of the *Protohaploxypinus* type with a distal sulcus. The wall structure of glossopterid pollen has not been studied in detail but is interpreted here as probably alveolar, similar to that of many conifers and cordaites.

Nothing is known of the male gametophyte, but germination apparently was distal. Limited information is available, however, concerning the female gametophyte, which was apparently cellular and contained either one (Gould & Delevoryas, 1977: 392) or two archegonia (Schopf, 1976: 56). The embryos of *Glossopteris* are unknown.

CAYTONIA

Sagenopteris leaves range from the Upper Triassic to Upper Cretaceous (Harris, 1951b, 1964), but knowledge of the *Caytonia* plant is based on a limited number of localities in east Greenland (Harris, 1933, 1937), eastern U.S.S.R. (Krassilov, 1977a), Poland (Reymanówna, 1973), Sardinia (Edwards, 1929), Sweden (Lundblad, 1948), and most importantly the Middle Jurassic of England (Thomas, 1925; Harris, 1940a, 1940b, 1941, 1945, 1951b, 1958, 1964). Three similar species are known from leaves, microsporophylls, and megasporophylls (Fig. 17, Table 8). The organs have never been found organically connected but are linked by association evidence, similarity of cuticular structure, and the consistent occurrence of *Caytonanthus* pollen in the micropyles of *Caytonia* ovules (Thomas, 1925; Harris, 1933, 1940a, 1941, 1951b, 1964). Other genera of reproductive structures that may be related to *Caytonia* (e.g., *Pramelreuthia* Kräusel, 1949; *Ktalenia* Archangelsky, 1963) are not included in this discussion of characters.

The stem of the *Caytonia* plant is known from several small twigs (Harris, 1940b, 1971), but they are sufficient to show that it was a woody shrub or tree with alternate leaves. The twigs were thicker than in most extant temperate trees and shrubs. They bore alternating zones of budscales and leaves. Buds occur in the axils of the leaves. Branching was sympodial, the apical bud ceasing to grow and being succeeded by two lateral buds to give forked branching as occurred for example in the bennettitalean *Wielandiella angustifolia* (Nathorst, 1909). The leaves (*Sagenopteris,* Fig. 17A, B) were borne on raised "leaf cushions" and had a long petiole bearing four narrowly elliptical leaflets at the apex. Although superficially palmate, the leaflets were arranged in two pairs (Fig. 17B). They each have a midrib and reticulate venation. Small leaves with broad stipule-like petiolar flanges and budscales also are known (Harris, 1940b). The leaves apparently were deciduous, with both leaflets and petioles shed. Stomata were anomocytic.

The megasporophylls (*Caytonia,* Fig. 17E) were pinnate, bearing lateral "cupules" on short stalks. It is not known how they were attached to the stem. The "cupules" were reflexed, with a small lip on one side close to the stalk. They were all borne on one surface of the rachis, and all were reflexed in the same direction. Differentiation of the cuticle suggests that the lips were on the upper (presumed adaxial) surface (Harris, 1940a). The cells around the lip were papillate (Thomas, 1925: 310). At maturity the "cupules" probably were fleshy and "berry-like" (Harris, 1951b) and shed individually. The "flesh" of the "cupule" consisted of a network of vascular strands, large

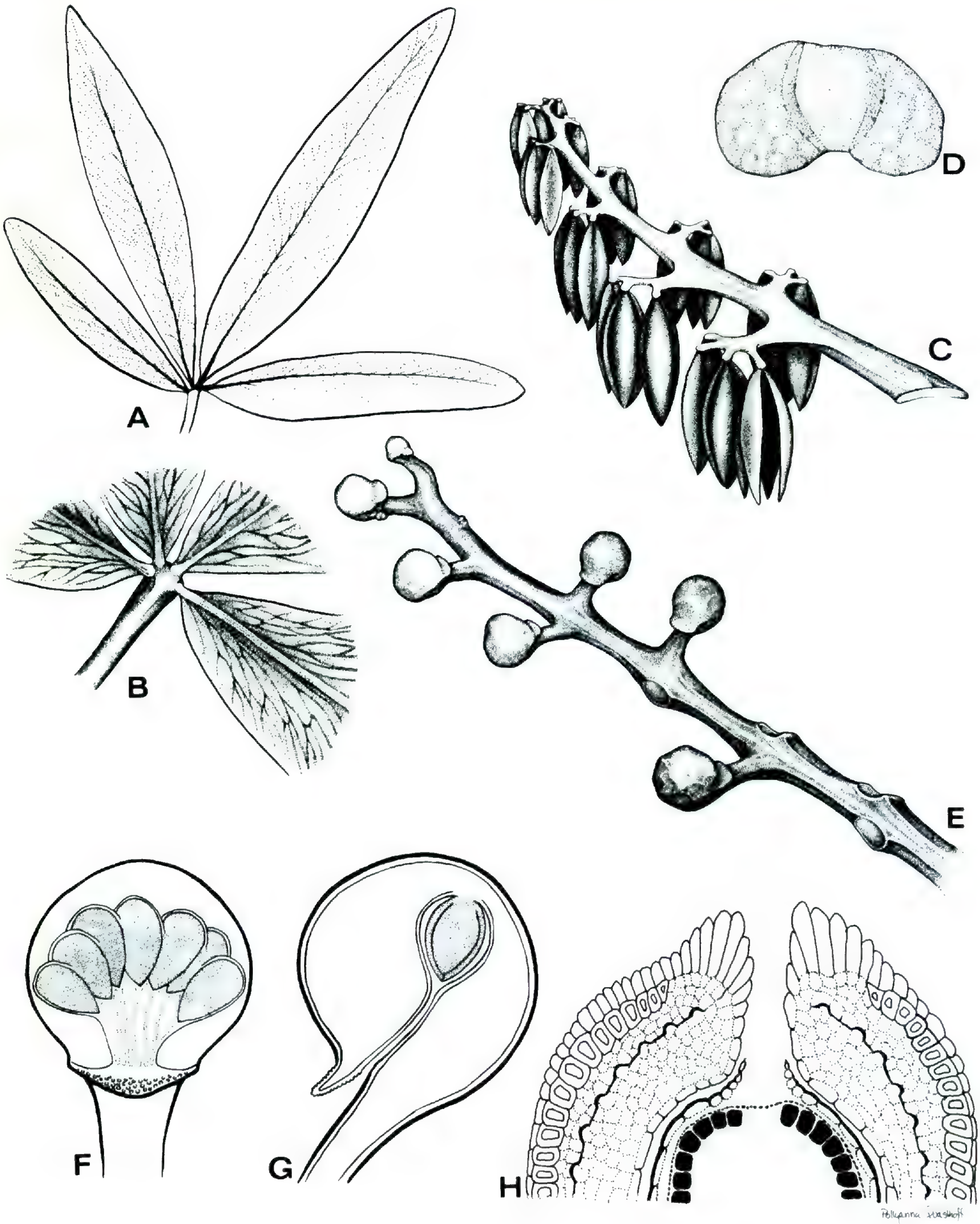


FIGURE 17. Morphology of the *Caytonia* plant.—A. *Sagenopteris colpodes,* based on Thomas (1925, pl. 15, fig. 50); ×0.75.—B. *S. colpodes,* detail of leaflet attachment and venation, based on Harris (1964, fig. 2H); ×4.—C. *Caytonanthus arberi,* based on Harris (1941, pl. 2, fig. 3); ×7.—D. Pollen from *C. arberi,* based on Townrow (1962b, fig. 3d, e); ×1,200.—E. *Caytonia nathorstii* megasporophyll, based on Harris (1964, fig. 10A–C); ×5.—F. *Caytonia* "cupule" containing seeds, based on Reymanówna (1973, particularly text fig. 12E, F); ×12.5.—G. *Caytonia* "cupule," longitudinal section, based on Reymanówna (1973, particularly text-fig. 12E, F); ×12.5.—H. *C. nathorstii* ovule longitudinal section, redrawn from Harris (1958, fig. 7); ×110.

TABLE 8. Isolated organs of the three best known species of the *Caytonia* plant (after Harris, 1941, 1951b).

Locality	Leaf	Megasporophyll	Microsporophyll
U.K., Yorkshire (M. Jurassic)	*Sagenopteris colpodes*	*Caytonia sewardi*	*Caytonanthus oncodes*
	Sagenopteris phillipsii	*Caytonia nathorstii*	*Caytonanthus arberi*
E Greenland (U. Triassic–L. Jurassic)	*Sagenopteris nilssoniana*	*Caytonia thomasii*	*Caytonanthus kochii*

rounded cells, and branched sclereids (Reymanówna, 1973). Each "cupule" contained a "packet" of several small ovules surrounded by a common cuticular membrane that was continuous with the outer cuticle of the cupule (Fig. 17F; Krassilov, 1977a; Reymanówna, 1973). The ovules were arranged with their micropyles oriented towards the mouth, below the lip of the "cupule." Narrow channels ran between the cuticles of the mouth connecting the micropyles with the outside (Fig. 17G).

The ovules were flattened and unitegmic, with a narrow micropylar slit (Harris, 1940a, 1958; Thomas, 1925). The integument was free from the nucellus except at the chalaza and was supplied by a pair of vascular bundles (Reymanówna, 1973). Each bundle consisted of scalariform tracheids that ran along the edge of the seed in the primary plane, almost to the micropyle. The integument and nucellus were strongly cutinized, but no acid-resistant megaspore membrane was detected (Fig. 17H; Harris, 1958).

The microsporophylls (*Caytonanthus,* Fig. 17C) were pinnate, with irregular, short, lateral "branches." It is not known how they were attached to the plant, but they were dorsiventrally flattened, with different cuticles on the upper and lower surfaces. On their lower surface the lateral "branches" bore radially symmetrical, elongated synangia, with four (rarely, three or five) locules. The locules dehisced longitudinally towards the inside, separating in the middle but remaining attached at the apex and base. The pollen (*Vitreisporites,* Fig. 17D) was bisaccate with a distal sulcus. Krassilov (1977a) has described monosaccate grains. The pollen wall was alveolate with large cavities (Crepet & Zavada, pers. comm.). Although *Caytonia* was claimed originally to be an angiosperm (Thomas, 1925), Harris (1933, 1940a) demonstrated *Vitreisporites* pollen in the micropyles of *Caytonia* seeds. Pollination probably involved a pollination drop mechanism that drew pollen along the channels of the mouth and onto the micropyles.

Nothing is known of the male or female gametophyte of *Caytonia,* and the embryo is only known from "aleurone cells" (Harris, 1958).

CORYSTOSPERMS

The Corystospermaceae was established by Thomas (1933) for leaves, microsporophylls, and megasporophylls from the Middle Triassic Molteno Beds of the Upper Umkomaas Valley, Natal (see Anderson & Anderson, 1983). Some of Thomas' specimens have been subsequently reinterpreted (Townrow, 1962a), and additional material has been described from the Molteno flora of Zimbabwe (Lacey, 1976), the Upper Triassic/Lower Jurassic of Tasmania (Townrow, 1965), the Triassic of New South Wales (Holmes & Ash, 1979), the Triassic of India (Pant & Basu, 1973, 1979; Srivastava, 1974), the Triassic of Argentina (Archangelsky, 1968; Petriella, 1979, 1980, 1981, 1983), and the Middle Jurassic of Yorkshire (Harris, 1964). The individual organs have never been found in organic connection but are treated together on the basis of consistent association, similarity of cuticular structure, and the occurrence of pollen from the microsporangia in micropyles of the ovules (Archangelsky, 1968; Harris, 1964; Thomas, 1933; Townrow, 1962a, 1965).

The corystosperms were woody plants, but their stems are poorly known. Harris (1983a) described the stem of *Pachypteris papillosa* based on compressions, and Archangelsky (1968) has suggested that *Rhexoxylon* (Fig. 18G; Archangelsky, 1968; Archangelsky & Brett, 1961) may be the stem of some Triassic corystosperms. Externally *Rhexoxylon* showed leaf bases and branch scars. It is not known whether axillary branching occurred. Internally there was a large pith surrounded by a ring of vascular segments with secondary xylem developed both centripetally and centrifugally in relation to the primary xylem. This "polystelic" arrangement may well be merely a modification of a basic eustele (Beck et al.,

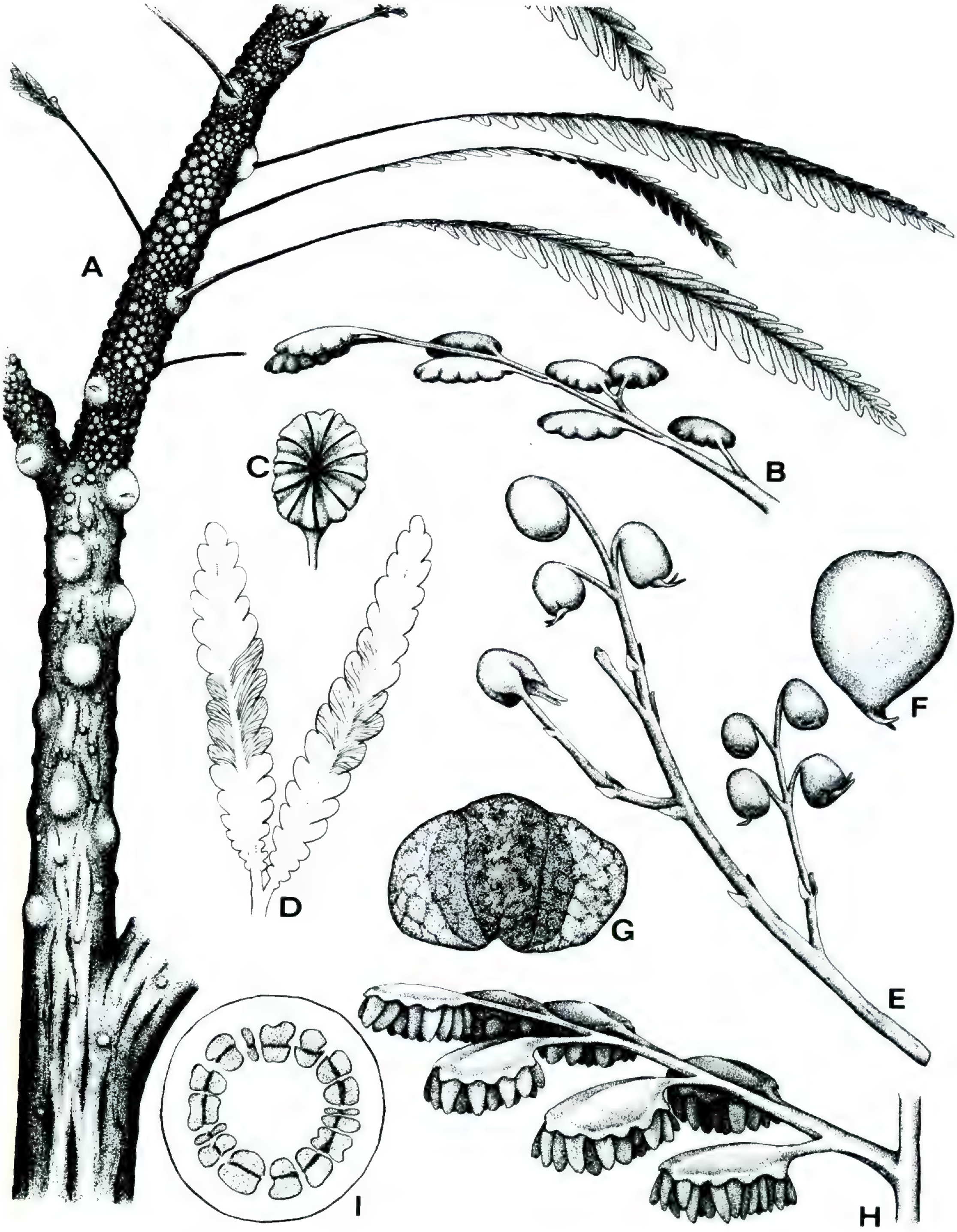


FIGURE 18. Morphology of corystosperms.—A. *Pachypteris papillosa* stem with leaves, based on Harris (1983a, fig. 2); ×0.25.—B. *Pteroma thomasii* synangium, abaxial view, redrawn from Harris (1964, fig. 66B); ×2.5.—C. *P. thomasii,* lateral view, based on Harris (1964, fig. 66A–G, I); ×2.—D. *Dicroidium odontopteroides,* redrawn from Thomas (1933, fig. 49a); ×0.75.—E. *Umkomasia macleanii,* redrawn from Thomas (1933, fig. 1, pl. 26, fig. 56); ×2.5.—F. Corystosperm ovule based on Thomas (1933, fig. 33c); ×4.—G. *Rhexoxylon,* transverse section of stem, based on Archangelsky and Brett (1961, fig. 2A); ×0.5.—H. Pollen of *Pteruchus africanus,* redrawn from Townrow (1962a, fig. 10F); ×600.—I. *P. africanus,* based on Townrow (1962a, fig. 1A–D); ×2.5.

1982; Stewart, 1983). The primary xylem contains tracheids with spiral thickenings or scalariform pitting. The secondary xylem segments were pycnoxylic, although some axial parenchyma occurred. The tracheids had uniseriate to triseriate, circular bordered pits on the radial walls. The rays were uniseriate (Archangelsky & Brett, 1961).

Corystosperm leaves have been referred to a variety of genera, including *Dicroidium* (Fig. 18D), *Xylopteris,* and *Pachypteris* (Townrow, 1965). The leaf rachis was generally forked, with a simple or bipinnate arrangement of pinnae (Retallack, 1977: 255; Townrow, 1965). Stomata were anomocytic.

Megasporophylls were dorsiventrally organized and branched in a single plane (Fig. 18E). They consisted of a main axis with irregularly positioned lateral "branches" bearing several recurved "cupules." Thomas (1933) described "bracts" and pairs of "bracteoles" on these structures, and he therefore interpreted them as fertile branches. However, a similar interpretation of the microsporangiate organs was not supported by Townrow (1962a), who showed the "bracts" to be sterile pinnules. The "cupule"-bearing structures never have been reinvestigated but are interpreted here as megasporophylls. It is not known how they were attached to the stem.

The megasporophylls were highly variable, and Thomas (1933) recognized three genera, based on branching pattern, the form of the "cupule," and the presence or absence of cupular hairs. In *Umkomasia* the "cupules" were divided into two lobes by clefts in the plane of branching, and lacked hairs or hair bases on the inner surface. *Pilophorosperma* had "cupules" with a single cleft and their inner surface covered by hairs. *Spermatocodon* had "cupules" with no conspicuous clefts, which lacked hairs on the inner surface. In all three genera each "cupule" contained a single ovule. Other subsequently described corystosperm "cupules" (e.g., *Karibacarpon,* Lacey, 1976; Holmes & Ash, 1979) also contain a single ovule.

The ovules were flat (Fig. 18F), and although their vasculature is unknown, they had files of small rectangular cells arranged in longitudinal rows along their two margins (Thomas, 1933: 229). At their apex the ovules had two elongated micropylar lobes that were curved to one side in the primary plane. The curved micropylar tube was oriented away from the cupule stalk. Detailed observations on the seed membranes of corystosperms still are needed, but Thomas (1933: 228) noted "a well cutinized testa" and an "exceedingly delicate inner membrane." The ovules are assumed to have been unitegmic, and the megaspore membrane probably was not well developed.

Microsporophylls (*Pteruchus,* Fig. 18I) were branched irregularly and bore groups of pendulous pollen sacs on expanded distal laminae. The "branches" (rachises, Townrow, 1962a) were attached either in a single plane (Townrow, 1962a) or spirally (Pant & Basu, 1973, 1979; Srivastava, 1974; Thomas, 1933). It is not known how the main axis was attached to the plant. Townrow (1962a) emphasized the leaf-like nature of *Pteruchus,* and it is interpreted here as a microsporophyll. Pollen sacs were ellipsoidal, unilocular, and dehisced along a single suture. Pollen was bisaccate (Fig. 18H), with a single distal sulcus, and very similar to that produced by *Caytonanthus* (Townrow, 1962b). The pollen wall was granular (Crepet & Zavada, pers. comm.; see also Taylor et al., 1984). Pollen has been described in the micropyle of one of the South African ovules (Thomas, 1933).

The microsporophyll *Pteroma thomasii* Harris (Fig. 18B, C) from the Middle Jurassic of Yorkshire also is included in the Corystospermaceae by Townrow (1965). On the basis of association and some similarity in cuticle, it is thought to be part of the *Pachypteris papillosa* plant (Harris, 1964). *Pteroma* is a pinnate structure with oval or round fertile laminae with a ring of microsporangia embedded in their undersurface. The microsporangia were unilocular, dehisced by a single longitudinal slit and produced bisaccate pollen.

Nothing is known of the male or female gametophyte, or embryo of corystosperms.

PENTOXYLON

Knowledge of the *Pentoxylon* plant is based mainly on silicified material from the Jurassic of the Rajmahal Hills, India. Sahni (1948) gave the most detailed account and linked the ovulate heads (*Carnoconites*) with the stem (*Pentoxylon,* Fig. 19D) and the leaves (*Nipaniophyllum,* Fig. 19C) on the basis of association evidence and structural similarity. Microsporangiate organs (*Sahnia,* Fig. 19E) were described subsequently by Vishnu-Mittre (1953), and knowledge of the *Pentoxylon* plant was reviewed by Rao (1976, 1981). The other published reports of *Pentoxy-*

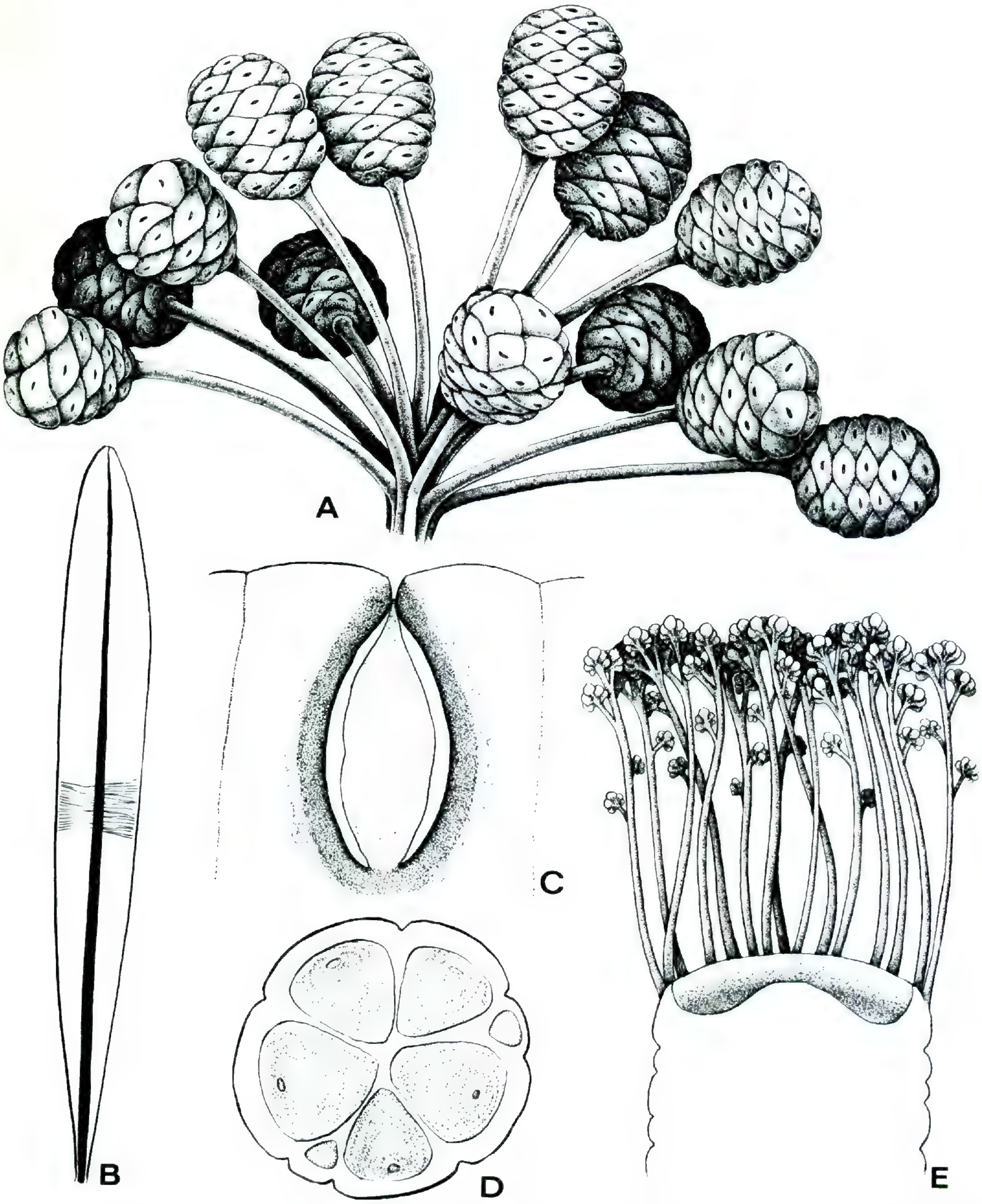


FIGURE 19. Morphology of *Pentoxylon* plants.—A. *Carnoconites cranwelliae,* ovulate heads, based on Harris (1962, text-fig. 2B, fig. 1); ×2.5.—B. *Carnoconites,* longitudinal section through ovule, based on Sahni (1948, fig. 21); ×10.—C. *Nipaniophyllum raoi,* redrawn from Sahni (1948, fig. 34a, b); ×1.—D. *Pentoxylon sahnii,* transverse section of stem showing vascular strands, based on Sahni (1948, fig. 9); ×8.—E. *Sahnia* microsporangiate "flower," based on Vishnu-Mittre (1953, fig. 11) and Bose et al. (in press); ×2.5.

lon are based on ovulate heads (Fig. 19A) and leaves preserved as compressions from the uppermost Jurassic or lowermost Cretaceous of New Zealand (Harris, 1962, 1983b) and a variety of different organs in the early Cretaceous of Victoria (Drinnan & Chambers, 1985), New South Wales (White, 1981), and Queensland, Australia (Turner, pers. comm.). The description given below and used in the phylogenetic analysis is based on both the silicified and compression material.

The stem (*Pentoxylon*) was differentiated into long and short shoots, both with helically arranged leaf-cushions showing leaf scars. In transverse section the stem typically had five vascular segments, but as in medullosans this is interpreted as a modification of a fundamentally eustelic arrangement (Beck et al., 1982: 749; Stewart, 1976). The secondary xylem was pycnoxylic with uniseriate rays and no axial parenchyma. Secondary xylem tracheids had uniseriate or biseriate circular bordered pits on their radial walls, although scalariform pitting has been reported in the microsporangiate structures and short shoots of *Sahnia* (Vishnu-Mittre, 1953). Leaf-traces arose in pairs, one from each of two adjacent vascular segments (Stewart, 1976). The leaves (*Nipaniophyllum*) were simple, strap-shaped, and of the taeniopterid-type, with a midrib and numerous pinnate veins. Stomata were originally described as "fundamentally Bennettitalean" (Sahni, 1948: 56), but many are apparently anomocytic, and the morphology and ontogeny of the stomata require detailed reexamination (Rao, 1976).

The ovules were sessile, orthotropous, helically arranged, and aggregated into compact ovoid (*Carnoconites compactum, C. cranwelliae*) or elongated heads (*C. laxum*). Each head of *C. compactum* consisted of about 20 ovules, but there were more in *C. cranwelliae* and *C. laxum*. No bracts or other structures were associated with these heads, nor were there interseminal scales as in Bennettitales. The ovulate heads were borne terminally on short shoots. In the Indian material a single pedicel produced several branches, each of which bore a single ovulate head. In the New Zealand material (*C. cranwelliae*) 12 separate pedicels arose from the same point in an umbel-like arrangement, and each bore a single ovulate head.

Ovules of *Carnoconites compactum* were flattened, with two integuments that were free from the nucellus except at the chalaza. The sclerotesta was bicarinate and distinctly flattened in transverse section. Immediately surrounding the sclerotesta was a distinct layer of dark cells. The remaining outer part of the "integument" formed a thick, fleshy "sarcotesta" interpreted here as an outer integument and probable "cupule" homologue (see character 9.19). Each ovule was supplied by a single vascular bundle that penetrated the sclerotesta at the chalazal end; no other vascular tissue has been reported in the ovules. The ovule cuticles of *C. compactum* and *C. laxum* are unknown, but in *C. cranwelliae* the sarcotesta had a thick outer cuticle. The inner cuticle of the integument was delicate but the nucellar cuticle was robust. There was no megaspore membrane preserved.

The microsporophylls (*Sahnia*) were borne in a whorl, or low helix, forming a "flower" around a broad, conical, sterile receptacle. They were surrounded themselves by deciduous bracts. According to Vishnu-Mittre (1953), the microsporophylls were fused proximally to form a shallow cup, but according to Rao (1981), they were free at the base. The microsporophylls were numerous, and each bore ten to 20 spirally arranged, stalked unilocular sporangia. The sporangia were borne singly or in groups of two or four. Each sporangium was pyriform and thick-walled, with monosulcate non-saccate pollen. Pollen wall stratification was probably granular (Taylor & Crane, in progress).

Monosulcate pollen has been described in the micropyles of *Carnoconites* ovules. Germination was apparently distal. Nothing is known of the male gametophyte, and Sahni (1948: 46) describes one poorly preserved specimen with what may be the remains of megagametophyte tissue. No well-preserved embryos have been described, although Harris (1962) mentions a flat, cutinized plate in *C. cranwelliae* seeds, which he tentatively interpreted as the remains of the "aleurone layer" of the "endosperm."

BENNETTITALES

An outline cladogram of the Benettitales already has been presented (Fig. 12). Knowledge of other characters is very uneven, and in this section a general description of the Bennettitales is synthesized from features preserved in the different taxa.

The Bennettitales exhibited considerable diversity in habit ranging from unbranched pachycaul forms (*Cycadeoidea, Monanthesia*) to forms that were more slender and highly branched (Delevoryas, 1975; *Ischnophyton,* Delevoryas & Hope, 1976; *Williamsonia leckenbyi* plant, Harris, 1969). The anatomy of highly branched forms is unknown, but in pachycaul plants there was a large pith and a single broad ring of vascular tissue. The primary vasculature was eustelic, and a bifacial cambium produced both secondary xylem and secondary phloem. The wood was dis-

sected into numerous segments by broad rays, but individual segments were pycnoxylic with only uniseriate or biseriate rays. Tracheidal pitting was highly variable (Bose, 1953) ranging from multiseriate circular bordered pits to scalariform pitting (Sahni, 1932a). Leaf-traces pass directly into the leaf and do not girdle the stem as in cycads (Crepet, 1974: 178). Axillary branching is known to have occurred. Leaves generally were pinnate (see character 6.10) although there was some variation (Ash, 1975), and in *Eoginkgoites* there were several pairs of pinnae at the apex of the petiole giving a pseudopalmate arrangement (Ash, 1976, 1977). Stomata were paracytic, with distinctive cuticular thickenings (see character 6.2).

Ovules were grouped into "flower-like" heads, generally with surrounding bracts forming a "perianth" (but see *Vardekloeftia,* character 6.5). The ovules were small, generally less than 7 mm long, and frequently only 1–2 mm. Ovules were radially symmetrical (although flattened in *Vardekloeftia* and *Bennetticarpus wettsteinii*), with two integuments that were free from the nucellus except at the chalaza (see p. 764). Frequently the nucellus was borne on a long stalk. Each ovule was supplied by a single vascular trace that ran to the base of the nucellus, but no other vasculature is known in the integument. Distally the integument was elongated into a long micropylar tube, and at maturity the integument was differentiated into four layers (Crepet, 1974: 157). The megaspore membrane was thin or not acid-resistant, but the cuticle of the nucellus and inner surface of the integument was well cutinized (Harris, 1954, 1969). The ovules were not individually subtended by any other organs but are surrounded by numerous sterile interseminal scales that develop from primordia of bitegmic ovules (see character 6.1). The interseminal scales generally have a single vascular bundle.

Microsporophylls were aggregated into "flower-like" heads surrounded by a "perianth" of bracts. The microsporangia are borne in various ways, but most of those known are aggregated into bivalved synangia (character 6.4). Pollen is monosulcate, boat-shaped, and more or less smooth-walled. The pollen wall is granular (*Cycadeoidea,* Crepet, pers. comm.; Taylor, 1973).

The multicellular male gametophytes reported by Wieland (1906) are now interpreted as internal folds in the pollen wall (Taylor, 1973). The female gametophyte apparently was monosporic, developing from the innermost of a linear tetrad of megaspores (*Cycadeoidea,* Crepet & Delevoryas, 1972). Little is known of the subsequent development in *Cycadeoidea,* but according to Sharma (1974), in *Williamsonia* free nuclear divisions were followed by cellularization beginning at the micropylar end and proceeding toward the base. Cellular dicotyledonous embryos are known in *Cycadeoidea* (Crepet, 1974; Wieland, 1906, 1916).

GNETALES

A cladogram for the Gnetales has been presented already (Fig. 4). Only a general description of the Gnetales is given here as a basis for assessing their relationship with other seed plants.

The stelar morphology of *Gnetum* and *Welwitschia* is poorly known, but in *Ephedra* the primary vasculature is a eustele (Beck et al., 1982: 757–759). In *Ephedra* there is a single ring of vascular bundles with secondary xylem and phloem, but in *Gnetum* and *Welwitschia* there may be several concentric rings. The secondary xylem tissue consists of tracheids with circular bordered pits, vessels, and axial parenchyma. Axillary branching occurs in all genera, but leaf morphology is variable, ranging from the reticulate veined leaves of *Gnetum* to the strap-shaped parallel veined leaves of *Welwitschia,* and the scale-like or needle-like leaves of *Ephedra.*

The morphology and arrangement of the ovulate and microsporangiate reproductive structures of the Gnetales have been discussed already. The ovules generally are small, and the innermost layer of the various ovular coverings generally is regarded as a single integument. It is "fused" with the nucellus for about half its length. Apically the integument forms an elongated micropylar tube. The ovules of *Gnetum* and *Welwitschia* are not obviously flattened, although in *Welwitschia* there are a pair of minute lateral flaps at the base of the non-functional ovule in the microsporangiate flower. In some species of *Ephedra* (e.g., *E. distachya*) the integument originates from a pair of dorsiventral primordia (Martens, 1971, fig. 24.4, 24.5), and at maturity there are two integumentary vascular bundles (Eames, 1952: 87). In some species of *Ephedra,* therefore, the ovules appear to be platyspermic, but the orientation of the primary plane is at 90° to the bract unlike the situation occurring in conifers. The acid-resistant megaspore membrane of mature seeds in the Gnetales is either ex-

tremely thin (about 1 μm) as in *Welwitschia* and *Ephedra* or lacking altogether in *Gnetum* (Erdtman, 1965; Thomson, 1905).

The microsporangiate structures of *Welwitschia* and some species of *Ephedra* are arranged in a whorl, although in *Gnetum* the microsporangia are borne on a solid structure (character 1.7). Gnetalean pollen has already been described (character 1.5), and the evidence currently available (Van Campo & Lugardon, 1973) suggests that the exine is comprised of a tectum, a granular interstitium, and a thick, laminated inner layer. Microgametophyte development (character 1.1) and megagametophyte development (characters 1.2, 1.3) in the Gnetales have already been described. Embryogenesis varies in the three genera. In *Ephedra* there is a short free nuclear phase, but in *Welwitschia* embryogenesis is completely cellular. In *Gnetum* there are reports of both a free nuclear phase and completely cellular embryogenesis (Martens, 1971: 265).

ANGIOSPERMS

Most estimates place the total number of angiosperm species at around 250,000–300,000. This enormous number, coupled with extreme morphological diversity and inadequate comparative knowledge, makes the angiosperms extremely difficult to deal with as a group in a broad cladistic analysis such as this (Hill & Crane, 1982). Although it is widely accepted that the Magnoliidae and some monocotyledons have retained a relatively large number of primitive characters, they are still an extremely heterogeneous assemblage within which it is difficult to come to definite conclusions concerning likely plesiomorphic features. This difficulty is well illustrated by the argument over whether the angiosperms are primitively vesselless (Young, 1981). In the case of the few higher dicotyledons that lack vessels, this can be reasonably hypothesized as secondary loss, but in the case of vesselless magnoliid plants, this is much more problematic. The issue can only be resolved by a well corroborated phylogenetic analysis of relationships within the primitive angiosperms (Riggins & Farris, 1983). Until such a phylogenetic hypothesis is available for primitive flowering plants, the analysis provided here can only be regarded as preliminary. Characters of flowering plants are considered individually as part of the character discussion given below.

PHYLOGENETIC RELATIONSHIPS OF EXTANT AND FOSSIL GYMNOSPERMS

ANALYSIS OF CHARACTERS

9.1 Eustele. Beck et al. (1982: 701) define a eustele as "a stele with a hollow cylinder or tubular mass of tissue (i.e., with or without definable pith) and with discrete sympodia usually either as a discontinuous cylinder or in a scattered and dispersed arrangement." This kind of stele occurs in *Archaeopteris* and most seed plants and contrasts with the protosteles or siphonosteles typical of pteridophytes, including the aneurophytalean progymnosperms (Beck et al., 1982: 726). Fossil taxa with unknown stem anatomy (peltasperms, *Caytonia*) are assumed for present purposes to have had a eustele. The angiosperms too are interpreted here as fundamentally eustelic although this has been disputed by Tomlinson (1984) particularly for the monocotyledons. A few seeds plants, however, are protostelic, particularly among the "lyginopterid seed ferns" (e.g., *Heterangium, Microspermopteris, Tetrastichia,* Taylor, 1981a). Out-group comparison with all pteridophytes, except *Archaeopteris,* suggests that this may be the primitive condition for seed plants as a whole. On this basis *Quaestora* probably exhibits the primitive medullosan condition, the "polystelic" eustele having evolved *within* the group. The medullosans are therefore treated as protostelic in this analysis.

9.2 Embryogenesis with a free nuclear phase. In extant bryophytes and pteridophytes all of the divisions of the zygote following fertilization involve the formation of cell walls (Sporne, 1970). Embryogenesis is cellular throughout. In embryos of extant cycads and *Ginkgo* a coenocytic phase with 250 or more nuclei may be produced before cellularization occurs. In *Ephedra* and most conifers there is a short free nuclear phase of approximately three zygotic divisions. The presence of a free nuclear phase in embryogenesis is interpreted (Hill & Crane, 1982) as a specialized feature of seed plants by out-group comparison with pteridophytes. In *Welwitschia* and angiosperms (Martens, 1971: 265) embryogenesis is cellular throughout. In *Gnetum* whether early embryogenesis is cellular or has a free nuclear phase is uncertain (Martens, 1971: 265). The primitive condition is assumed in this analysis. A few conifers have wholly cellular embryogenesis (e.g., *Sequoia,* Martens, 1971: 265), but these taxa are specialized within the

conifer clade (Miller, 1982). I interpret this feature as a secondary advance within the group. As Chamberlain (1935: 342) suggested, there may be a correlation in seed plants between egg-cell size and the duration of the free nuclear phase. Embryogenesis for all fossil seed plants considered is unknown but is treated here as having involved a free nuclear phase. In *Archaeopteris,* however, in line with other presumed pteridophytic aspects of its reproductive biology (Pettitt, 1970), I have treated embryogenesis as being cellular throughout.

9.3 Single functional megaspore mother-cell per megasporangium. With the exception of *Archaeopteris* the megasporangium in all of the taxa considered here produces one functional megaspore mother-cell. In all seed plants except *Gnetum, Welwitschia,* and a few angiosperms (character 9.28) one functional megaspore is subsequently formed, and the remaining three megaspores abort. Under this interpretation the female gametophyte develops entirely within the megaspore, and the tissues of the megasporangium are regarded as homologous with the nucellus. In heterosporous species of *Archaeopteris* and most heterosporous pteridophytes (e.g., *Selaginella*) more than one megaspore is produced in each megasporangium. A few pteridophytes such as the extant fern *Marsilea,* the fossil lepidodendroid genera *Achlamydocarpon* and *Lepidocarpon,* the probable herbaceous Pennsylvanian lycopod *Miadesmia,* and the fossil sphenopsid *Calamocarpon* also have a single functional megaspore per megasporangium, but the distribution of other characters (not analyzed here) indicates that these are not homologous with the seed plant situation. This is the widely accepted view (Stewart, 1983).

9.4 Integument. All of the taxa considered in this analysis except *Archaeopteris* have the megasporangium (nucellus) surrounded by an integument. This feature has been given various interpretations in different groups of seed plants (see characters 9.7, 9.19), but no comparable structure occurs in extant pteridophytes. Enclosure of the megasporangium in the fossil lycopods *Lepidocarpon* and *Miadesmia* is achieved by lateral extensions of the megasporophyll that extend around the equator of the megaspore. This is not homologous with the situation in seed plants (Stewart, 1983) where enclosure has apparently occurred along the polar axis of the megaspore.

9.5 Micropyle. All seed plants considered in this study have a clearly defined micropyle, and although the integument may have a pair of lateral "horns" (e.g., conifers, *Ginkgo*) or be elongated to form a long micropylar tube (e.g., corystosperms, Bennettitales, Gnetales), it is never deeply lobed around the micropyle as in early seed plants such as *Archaeosperma* (Pettitt & Beck, 1968; Pettitt, 1970). I interpret the unlobed micropyle as a derived feature that unites all the seed plants considered in this study (see also Stewart, 1983). *Archaeosperma,* the early seeds described by Gillespie et al. (1981), *Genomosperma kidstonii,* and *G. latens* (Long, 1959) all have a poorly differentiated micropyle that I interpret as the primitive condition. The lobed micropyle of some angiosperms (e.g., *Hernandia*) is clearly not homologous with the condition in early seed plants.

9.6 Linear tetrad of megaspores. Meiosis of the megaspore mother-cell in all extant seed plants produces a linear tetrad of megaspores of which only the inner develops, or female gametophyte development is tetrasporic (*Gnetum, Welwitschia,* and a few angiosperms, character 9.28). Most angiosperms produce a linear tetrad (Sporne, 1974: 162). In the fossil taxa considered in this study probable linear tetrads of megaspores have been described only in *Cycadeoidea* (Crepet, 1974; Crepet & Delevoryas, 1972), but the absence of haptotypic markings on the megaspores of all other taxa where this has been examined suggests that they also may have been produced in linear tetrads. Comparison of *Lyginopteris* with other "lyginopterid seed ferns" suggests that the megaspores may have developed from a tetrahedral tetrad. By out-group comparison with megaspores of pteridophytes and early seed plants (e.g., *Archaeosperma,* Chaloner & Pettitt, 1964; Pettitt, 1970) I interpret *Lagenostoma* (*Lyginopteris*) as primitive in this character.

9.7 Double vascular supply to ovules. Cycads and medullosans both have large ovules, which are supplied by a radially arranged double vascular system. The outer ring of bundles supplies the sarcotesta. In medullosans, the nucellus and integument are free except at the chalaza, and the inner ring of bundles supplies the nucellus; but in cycads where the nucellus is "fused" to the integument for most of its length, it is rarely clear whether the inner bundles are in nucellar or integumentary tissue. This double vascular supply to the ovules is not known to occur in any of the other taxa considered in this study.

Rodin and Kapil (1969) have compared the ovule vasculature of *Gnetum* with that of *Pachy-*

testa, but under the interpretation given here (character 9.33) only the inner envelope of a *Gnetum* ovule is a true integument, and therefore the two outer layers do not have homologues in cycads or medullosans. In *Lagenostoma* (*Lyginopteris*) there is a unitegmic ovule with a radial vascular supply inside a vascularized cupule. It has been suggested (Sporne, 1971a: 61; Wordsell, 1906) that this cupule may be homologous with the integument of cycads and medullosans and that their inner vascular system represents the remains of an "inner" integument. However, the "inner" integument of *Lagenostoma* is differentiated into a sarcotesta, a sclerotesta, and endotesta as in most gymnosperm seeds, including those of cycads and medullosans. There is no evidence in cycads and medullosans, other than the vasculature, for an additional tissue layer in the integument, and the "double integument" interpretation is not accepted in this paper (see also Stewart, 1983). Similarly the pad of vascular tissue at the base of *Cardiocarpus* and *Mitrospermum* ovules is not taken to indicate the former presence of an "inner integument" (Graham, 1935). In peltasperms and corystosperms ovule vasculature is unknown but assumed not to have been double as in cycads and medullosans.

Only the inner integument of angiosperms is interpreted in this study as homologous to the integument of other seed plants (character 9.19). Very few angiosperms have a vascularized inner integument (Sporne, 1974: 154), and I know of none in which a double vascular system has been described.

9.8 Axillary branching. Despite intensive study of anatomically preserved material, axillary branching has not been reported in progymnosperms. Axillary branching has also never been demonstrated in extant cycads (p. 744). In all other plants considered in this study axillary branching is either known or is assumed (peltasperms, corystosperms) to have been present.

9.9 Saccate pollen. Saccate pollen or prepollen is generally regarded as the primitive condition in conifers and cordaites, but also occurs in *Callistophyton*, glossopterids, *Caytonia*, and corystosperms. Saccate pollen is interpreted as a relatively specialized feature within seed plants, although it should be noted that saccate spores occur in some aneurophytalean progymnosperms (e.g., *Rellimia, Tetraxylopteris*; Bonamo, 1977; Bonamo & Banks, 1967; Leclerq & Bonamo, 1971; Scheckler & Banks, 1971) and Pennsylvanian lycopods (Kosanke, 1969; Pigg & Rothwell, 1983). Saccate pollen reported in medullosans (*Parasporites* in *Parasporotheca* Dennis & Eggert, 1978) is treated here as specialized *within* that group.

9.10 Flattened ovules. Flattened ovules with one or two planes of symmetry occur in conifers, cordaites, *Callistophyton*, and all of the "Mesozoic seed ferns" (peltasperms, glossopterids, *Caytonia*, corystosperms, *Pentoxylon*). Flattened ovules also occur in some lyginopterid seed ferns (not *Lagenostoma*) that are too poorly known to evaluate their relationships further (e.g., *Lyrasperma*, Long, 1960). In cordaites, conifers, *Callistophyton*, *Caytonia*, and *Ephedra* there are two vascular bundles in the primary plane that run in the sarcotesta for most of their length, but in *Ginkgo* the bundles run within the endotesta. In the Bennettitales the ovules are small, with no integumentary vascular tissue, and are generally regarded as radiospermic. However, in the primitive bennettitalean genus *Vardekloeftia* (Figs. 9B, C, 12) and in the Upper Triassic *Bennetticarpus wettsteinii* (Kräusel, 1949), the ovules are relatively large (7–10 mm long) and flattened. More detailed examinations of the ovules in primitive Bennettitales are required, but here I interpret this platyspermy as primitive for the Bennettitales on the basis that the ovules resemble those of Mesozoic seed ferns, *Callistophyton*, cordaites, and other groups mentioned above. The integument of *Gnetum* ("endotesta" of Rodin & Kapil, 1969) has a well-developed radial vascular system; and *Welwitschia* ovules are unvascularized and radiospermic.

The bitegmic ovules of many angiosperms are bilaterally symmetrical and anatropous. However, if the interpretations accepted in this paper are correct (character 9.19), then this is homologous to a flattened recurved "cupule" containing a single unitegmic ovule. A comparable situation occurs in the corystosperms, and in this group the primary plane of the ovule is aligned in the same plane as the "cupule" stalk. Although many bitegmic ovules of angiosperms could be flattened "cupules," each containing a flattened seed, there is no convincing evidence that the nucellus and inner integument of angiosperm ovules are fundamentally platyspermic.

9.11 Megaphyllous leaves organized on a pinnate plan. Megaphyllous pinnately organized leaves occur in all taxa considered except *Archaeopteris*, cordaites, conifers, *Ginkgo*, *Welwitschia*, and *Ephedra*. In these taxa leaf vena-

tion is either univeined, dichotomous and diverging, or dichotomous and basically parallel. Although reticulations do occur they are not well developed. In angiosperms the parallel or dichotomously veined leaves of *Kingdonia, Circaeaster,* and many monocotyledons (Foster & Gifford, 1974) are interpreted as secondary advances within the angiosperm clade. Megaphyllous leaves are not known to occur in progymnosperms.

9.12 Narrowly triangular awl-shaped leaves. This feature already has been discussed in relation to conifers (character 3.1). The triangular leaves in *Ephedra* and a few, presumably derived, angiosperms are only superficially like those of conifers, but in *Cordaixylon, Mesoxylon, Lyginopteris,* and *Callistophyton* scale-like leaves similar to those of conifers are occasionally produced on proximal parts of branches and associated with axillary buds (Rothwell, 1982a). These heteroblastic leaf series may be important in the origin of conifer foliage (Rothwell, 1982a), but in this analysis the *consistent* production of narrowly triangular awl-shaped leaves only occurs in *Lebachia* and extant conifers.

9.13 Megasporophylls borne on short fertile shoots in the axil of a bract or leaf. This feature already has been discussed in relation to conifers (character 3.3). The megasporophylls of conifers, cordaites, and *Ginkgo* are all borne on fertile shoots in the axil of a bract or leaf. In the Gnetales the ovules are terminal. In peltasperms, *Caytonia,* and corystosperms it is not known how the megasporophylls were attached to the plant, but from their morphology it is unlikely that they were borne in a manner homologous with that of cordaites and conifers, and the unspecialized condition is assumed. In glossopterids (character 4.2) the megasporophylls were adnate to a subtending leaf or bract, but the morphological situation and homologies are unclear.

The interpretation of this character in flowering plants is dependent on whether the angiosperm carpel is regarded as a modified simple megasporophyll (e.g., Doyle, 1978) or a compound structure formed from a fertile branch in the axil of a subtending leaf or bract (e.g., Stebbins, 1974). This paper adopts the former interpretation (character 9.34). In some angiosperms (e.g., "Amentiferae," Chloranthaceae) the carpels are borne in the axil of a bract or leaf, but this is generally regarded as a secondary advance within the angiosperm clade (Walker & Walker, 1984).

9.14 Fertile axillary ovulate shoots aggregated into an "inflorescence." The fertile axillary ovulate shoots of cordaites and conifers are aggregated into an "inflorescence," but in *Ginkgo* the fertile axillary shoot is single in the axil of a leaf. The situation in cordaites and conifers is not known to occur in other seed plants considered in this study. The relationships of the enigmatic Southern Hemisphere conifers *Buriadia* and *Walkomiella,* and the possibility that they represent "the coneless ancestors of *Lebachia*-like conifers" (Pant, 1977b: 31) is not examined in this paper, although it is of interest to note that they may post-date *Lebachia* in the fossil record (Rothwell, 1982a; Pant, 1977b).

9.15 Pollen with distal germinal aperture. Pollen with a distal aperture (and therefore, presumably, distal germination) occurs in all of the seed plants considered here, with the exception of medullosans, *Lyginopteris,* and *Mesoxylon,* where the aperture is proximal (prepollen; Schopf, 1938; Chaloner, 1970a). Outgroup comparison with pteridophytes suggests that distal germination is a derived feature. The pollen of *Lebachia* (*Potonieisporites*) has a proximal monolete suture but also frequently has two curved folds in the exine of the distal surface (Scott & Chaloner, 1983). However, material described by Mapes and Rothwell (1984) suggests that germination in *Potonieisporites* was proximal. In the Gnetales the distal aperture of *Welwitschia* is accepted as the primitive condition in the group relative to the inaperturate grains of *Ephedra* and *Gnetum* (character 1.5).

Although a few angiosperms have a proximal germinal aperture (Walker, 1974b), distal germination is widely considered to be primitive in the group (Chaloner, 1970a; Doyle, 1978; Walker, 1974b), equatorial germination being a subsequent development within the clade (Doyle, 1978).

9.16 Cordaites *foliage.* The characteristically strap-shaped foliage of *Cordaites* is known attached to *Cordaixylon dumusum* (Rothwell & Warner, 1984) and *Mesoxylon priapi* (Trivett & Rothwell, 1985). The leaves have dichotomous, more or less parallel veins and a characteristic internal anatomy with well-developed longitudinal fibrous ribs (Harms & Leisman, 1961). The leaves of *Welwitschia* are superficially similar but grow continuously from a basal meristem, and have much less well-developed sclerotic tissue (Martens, 1971: 94).

9.17 Primary axis of ovulate and microspo-

rangiate "inflorescences" dorsiventrally flattened with bracts and fertile shoots four-ranked. This character occurs only in *Cordaixylon* and *Mesoxylon* among the taxa studied.

9.18 Siphonogamy. Zooidogamy occurs in extant cycads and *Ginkgo.* All spores of living plants with proximal germination produce motile gametes (bryophytes, pteridophytes). This is the basis for inferring zooidogamy in those fossil taxa with proximal germinal apertures in their pollen (medullosans, *Lyginopteris, Mesoxylon, Lebachia*). *Callistophyton* is known to have produced a distal pollen tube, which was probably involved in gamete transfer. In this analysis all other fossil plants with distal germinal apertures in the pollen are scored uniformly as plesiomorphic in this feature.

9.19 Ovules borne in a "cupule." The ovules of glossopterids, *Caytonia,* and corystosperms are enclosed or partly enclosed by the megasporophyll lamina to form a "cupule." These Permian and Mesozoic "cupules" have frequently been compared, or considered homologous, to the cupules of Upper Devonian, Mississipppian and Pennsylvanian seed ferns, such as *Archaeosperma* and *Lyginopteris* (Thomas, 1933, 1955; Townrow, 1960). Morphologically, however, there are at least two different kinds of structure. The cupules of *Lyginopteris* and other early pteridosperms are axially organized with respect to the long axis of the ovules they enclose. The stalk is axially attached and the construction of the cupule may reflect an origin either from sterile axes ("telomes") or the ultimate segments of a deeply divided leaf (e.g., *Archaeopteris*). In glossopterids, *Caytonia,* and corystosperms, the stalk of the cupule is lateral with respect to the long axis of the enclosed ovules. This lateral arrangement is most easily interpreted as reflecting an origin from modified pinnae or pinnules, such as those of *Autunia,* which have become rolled or expanded in various ways to form "cupular" pouches. Doyle (1978: 383) expressed a similar view that the "cupules" of Permian and Mesozoic seed ferns are more easily explained as "leaflets modified by various degrees of circinnate enrollment than as direct homologues of the bell-shaped cupules of lyginopterids."

According to the interpretation of "cupules" in *Caytonia,* corystosperms, and *Glossopteris* given above, the bitegmic ovule of angiosperms may be interpreted as a uniovulate "cupule." The idea that the outer integument in a bitegmic angiosperm ovule is homologous to the "cupule" of "Mesozoic seed ferns" has been advocated by numerous authors (Doyle, 1978; Stebbins, 1974; Stewart, 1983). This view is supported by the recurved "anatropous" arrangement of the "cupule" in *Caytonia* and corystosperms, the zigzag micropyle of many bitegmic angiosperm ovules, and evidence that the funicle, chalaza, and outer integument are part of a single developmental unit (Bor, 1978), while the inner integument and nucellus are part of another. The complex net-like vasculature of the outer integument of many angiosperm ovules is a further similarity with the "cupules" of "Mesozoic seed ferns." The homology of the "cupules" of *Caytonia* and corystosperms with angiosperms is accepted in this paper as providing the most straightforward explanation of the second integument that does not require a de novo origin (cf. Long, 1966). Unitegmic ovules occur in relatively specialized flowering plants and are interpreted as a secondary development within the angiosperm clade.

In *Pentoxylon* and Bennettitales the homologies of the outer integument are more difficult to determine. In *Vardekloeftia* and *Bennetticarpus crossospermus* (Bennettitales) there is a distinct outer layer around the inner integument, which has been variously termed the "cupule" or "micropylar plate" (Harris, 1932b) and is interpreted here as the outer integument of a bitegmic ovule. In *Vardekloeftia* two seeds occasionally occur within a single "cupule," and this may indicate derivation from a structure that formerly contained more than one ovule (Harris, 1932b: 108). In *Cycadeoidea* Wieland (1906: 120) has described a "cup-shaped supporting basal husk," and in *Bennettites albianus* Stopes (1918) has described a "cupule or aril of elongated tubular cells." I suggest that both of these layers are homologous with the "cupule" of *Vardekloeftia* and *Bennetticarpus crossospermus* and the outer layer of *Bennetticarpus wettsteinii* seeds (Kräusel, 1949). In *Pentoxylon* I interpret the bennettitalean "cupule" as represented by the well-developed outer fleshy "sarcotesta" around each ovule, and the cuticle obtained from this layer in *Pentoxylon cranwellii* has been compared with that of the "cupule" in *Vardekloeftia* (Harris, 1962: 24).

On the interpretations of "cupules" given above the outer integument in the ovules of Bennettitales and *Pentoxylon* may be interpreted in three different ways. Either it is homologous with the cupule of *Lagenostoma* (*Lyginopteris*), or ho-

mologous with the "cupule" of glossopterids, *Caytonia,* corystosperms, and angiosperms, or it is independently derived and not homologous to either. In this paper I exclude the first possibility. Although the ovules of Bennettitales, *Pentoxylon,* and *Lagenostoma* are all orthotropous, they differ considerably in other features. The cupule of *Lagenostoma* is lobed, heavily vascularized, does not enclose the ovule, and is thought to have been borne on well-developed megaphylls. "Cupules" of primitive Bennettitales and *Pentoxylon* are unlobed, unvascularized, enclose the ovule, and are not borne on megaphylls.

The two remaining possibilities are considered by two different methods of scoring in the data matrix for this paper. In one analysis (cladogram 1, p. 770), the bennettitalean and *Pentoxylon* ovule is interpreted as non-homologous with the "cupules" of glossopterids, *Caytonia,* and corystosperms. In the second analysis (cladogram 2, p. 770) the homology of these different "cupules" (but not the cupule of the *Lyginopteris* plant) is accepted. The details of adjusting the data matrix for these two different interpretations are discussed later in the paper (p. 774).

In the Gnetales the only morphological features that may be interpreted as evidence for the presence of a "cupule" are the regular development of two nucelli within a single integument in some species of *Ephedra* (Thoday & Berridge, 1912), the two lateral flaps of tissue at the base of the non-functional ovule in microsporangiate "flowers" of *Welwitschia,* and the occasional occurrence of *Gnetum* ovules with four "integuments" (Pearson, 1915). In the absence of better evidence the Gnetales are treated as lacking a "cupule" in this analysis.

9.20 Megaspore membrane thin. Comparative information on the megaspore membranes of gymnosperms is inadequate. Currently available data suggest that a thick, well-developed acid-resistant megaspore membrane, like that typical of pteridophytes, is primitive within seed plants (Hill & Crane, 1982) and that the weakly developed membrane in *Caytonia,* corystosperms, *Pentoxylon,* Bennettitales, and angiosperms is a specialized condition (Erdtman, 1957, 1965; Harris, 1954; Thomson, 1905). The megaspore membrane in these plants is only weakly resistant to maceration, and frequently this seems to be correlated with the presence of a well-developed nucellar cuticle (Harris, 1954). In conifers the megaspore membrane varies in thickness between genera. A thin megaspore membrane, however, is most common in relatively advanced taxa (Erdtman, 1965; Miller, 1982). In angiosperms the megaspore membrane can be detected with transmission electron microscopy (Mogensen, 1978) but is not acid-resistant.

9.21 Granular pollen wall. The pollen of all the seed plants considered here has two well-defined wall layers, the outer of which is either alveolar or granular in construction (Doyle et al., 1975). Within the alveolar forms there are two basic types; one in which the alveolae are comprised of small, typically densely crowded cavities ("cycad type," Doyle et al., 1975), the other in which the alveolae are larger and more highly organized ("pinaceous type," Doyle et al., 1975). The microspores of *Archaeopteris* (Pettitt, 1966) and the pollen of corystosperms, Bennettitales, and Gnetales all have a granular wall structure. Pollen of cycads and medullosans is of the alveolate type, with small cavities, and the pollen of conifers, cordaites, *Ginkgo, Callistophyton,* peltasperms, glossopterids, and *Caytonia* is of the more highly differentiated alveolate type (Crepet & Zavada, pers. comm.; Doyle et al., 1975; Millay & Taylor, 1976). Pollen of *Lyginopteris* has not been studied with transmission electron microscopy but is assumed to have had a homogeneous wall as in the pollen of *Crossotheca.* Pollen of *Pentoxylon* is currently under investigation (Taylor & Crane, in progress). Preliminary results from transmission electron microscopy suggest that the pollen wall is granular.

Granular pollen wall stratification occurs in many angiosperm groups, and in most cases (e.g., Juglandaceae, Betulaceae) it is interpreted as a secondary modification within flowering plants. However, granular exines also occur in many magnoliid families (e.g., Amborellaceae, Annonaceae, Canellaceae, Magnoliaceae) (Walker, 1976). Walker (1976: 278) suggests that these granular exines represent a stage in the origin of tectate wall structure from a homogeneous, walled, atectate primitive condition. However, in the gymnosperms studied in this analysis a homogeneous exine occurs only in *Lyginopteris,* and the basic pollen wall type appears to be the alveolar condition with granular exines a relatively specialized feature seen in corystosperms, Bennettitales, Gnetales, and, presumably as a secondary advance, in some conifers (e.g., Araucariaceae, Taxodiaceae). In the context of seed plants as a whole, I accept the hypothesis that

granular pollen wall stratification is primitive within angiosperms (see also Doyle, 1978: 375–376).

9.22 Uniovulate "cupule." The "cupules" of *Caytonia* and the glossopterids considered here contain several ovules. In the glossopterid *Denkania* (Pant, 1977a; Surange & Chandra, 1975) the "cupules" apparently contain a single ovule, but this is interpreted as a specialized feature within the glossopterid clade. According to the interpretation of character 9.19, the corystosperms, Bennettitales, *Pentoxylon,* and angiosperms also have a single ovule per "cupule." The homologies of "cupules" in all of these taxa are treated in two different ways (p. 770) but are not considered homologous with the cupules of *Lyginopteris* and other early seed ferns, for reasons given earlier (character 9.19).

9.23 Microsporophylls forming "flowers." The microsporophylls of the Bennettitales, *Pentoxylon, Ephedra,* and *Welwitschia* are aggregated together in a whorl or pseudowhorl to form cup-like "flowers" quite distinct from the pollen cones of conifers. In Bennettitales, *Welwitschia, Ephedra,* and angiosperms they are clearly arranged in a whorl or tight helix (see also character 9.33). The microsporophylls are similarly aggregated in *Pentoxylon* but details of their arrangement are uncertain. It is not known how the microsporophylls of corystosperms, *Caytonia,* glossopterids, and *Peltaspermum* were arranged on the plant, but in this analysis I have assumed that they were not aggregated into "flowers" (plesiomorphic condition).

9.24 Uniovulate "cupule" erect. The uniovulate "cupules" of corystosperms like the multiovulate "cupules" of *Caytonia* were recurved, and I interpret this as the primitive condition (see character 9.19). In Bennettitales and *Pentoxylon* the uniovulate "cupules" are borne erect. In flowering plants the most widespread, and apparently primitive, configuration for the bitegmic ovule is anatropous. This is consistent with derivation of the outer integument from a recurved *Caytonia*-like or corystosperm "cupule." Although orthotropous bitegmic ovules do occur, these are considered as specializations within the flowering plant clade.

9.25 Megasporophylls "unicupulate." In the Bennettitales and *Pentoxylon* the presumed homologues of the megasporophylls consist of a single "cupule" (character 9.19). In other Permian and Mesozoic plants with "cupules" (*Caytonia* and corystosperms) there are several "cupules" per megasporophyll, and in *Glossopteris* this is also interpreted as the primitive condition (character 4.5).

In angiosperms the primitive carpel appears to be conduplicate, containing several seeds (Bailey & Swamy, 1951). Under the interpretation adopted in this paper, each carpel would therefore consist of several cupules, perhaps originating in the manner suggested by Doyle (1978). Although some of the carpels in the Magnoliidae (e.g., Chloranthaceae) contain only a single ovule, they are interpreted here as a secondary modification within flowering plants (Walker & Walker, 1984).

9.26 "Unicupulate" megasporophylls aggregated to form heads. In *Pentoxylon* and Bennettitales the "unicupulate" megasporophylls (characters 9.19, 9.25) are aggregated together to form heads. No comparable arrangement occurs in any other seed plant considered in this analysis.

9.27 Male gametophyte of three or four nuclei. In gymnosperms, a male gametophyte of four nuclei occurs only in *Gnetum, Welwitschia,* and some conifers (character 1.1). In angiosperms the male gametophyte is even less extensive and undergoes two mitotic divisions to produce three cells.

9.28 Female gametophyte tetrasporic. In *Gnetum* and *Welwitschia* (character 1.2), the female gametophyte is tetrasporic. Tetrasporic megagametophytes are uncommon in angiosperms (Sporne, 1974: 162) and are interpreted as a secondary development within the flowering plant clade.

9.29 Archegonia absent. As in *Gnetum* and *Welwitschia* (character 1.3), no archegonia are differentiated in the female gametophyte of angiosperms. However, the megagametophytes in these two groups differ markedly in both development and mature structure. For these reasons they are not accepted a priori as homologous in this analysis.

9.30 Embryo with "feeder." There is no structure comparable to the "feeder" of *Gnetum* and *Welwitschia* (character 1.4) in the embryo of angiosperms or any other seed plant.

9.31 Ribbed pollen. Ribbed pollen superficially similar to that of *Ephedra* and *Welwitschia* (character 1.5) occurs in some angiosperms (e.g., *Spathiphyllum,* Araceae; Trevisan, 1980). However, transmission electron microscopy shows that the ribs in *Spathiphyllum* are formed by a tectate columellate wall rather than by granular

exine as in *Ephedra* and *Welwitschia* (Trevisan, 1980). Ribbed pollen known to occur in Acanthaceae is also interpreted as a secondary development within the angiosperm clade.

9.32 Vessels with porose perforation plates. Vessels occur in the Gnetales (character 1.6) and most angiosperms. Although they have also been reported in the Bennettitales (Krassilov, 1984) they are not known to be general within that group. Typically the vessels of Gnetales and angiosperms have been regarded as independently derived from tracheids, with circular bordered pits and scalariform pitting, respectively (Cronquist, 1968). It also has been generally accepted that vessels arose *within* the angiosperms and that magnoliid angiosperms that lack vessels are primitively vesselless. However, Young (1981) has recently questioned whether the angiosperms are primitively vesselless. His analysis of relationships within the Magnoliidae suggests that it is more parsimonious to invoke loss of vessels rather than the multiple vessel origins, but this should not be taken to imply that angiosperm and gnetalean vessels are necessarily homologous. Muhammad and Sattler (1982), however, have described "scalariform" and "sclaroid" perforation plates in *Gnetum,* which further blur the distinctions between angiosperm and gnetalean vessels.

Despite these difficulties the traditional view, that vessels of Gnetales and angiosperms are nonhomologous, is adopted in this paper. A more detailed evaluation of relationships within the Magnoliidae is required to evaluate the systematic position of vesselless taxa. Also, the similarities in perforation plates, of *Gnetum* and angiosperms described by Muhammad and Sattler (1982), involve taxa that are regarded as relatively derived within flowering plants (e.g., various "Amentiferae").

9.33 Microsporangiate and ovulate "flowers" with opposite pairs of bracteoles. The reproductive structures of the Gnetales and several angiosperm groups are arranged on an opposite and decussate plan (character 1.7). In many cases, such as the "Amentiferae," this arrangement is thought to be a secondary modification within the flowering plant clade. This probably also is the case in more primitive angiosperms such as Chloranthaceae (Walker & Walker, 1984, fig. 111).

9.34 Bitegmic ovule enclosed or partially enclosed by a structure with a pollen-receptive stigmatic surface external to the second integument. Several living and extinct gymnosperms show total or partial enclosure of a unitegmic ovule (e.g., *Caytonia,* corystosperms, Bennettitales, glossopterids, and some conifers), and some (e.g., *Tsuga* and perhaps *Leptostrobus*) have a pollen-receptive surface external to the micropyle. However, no known gymnosperm has an enclosed, or partially enclosed, bitegmic ovule and a pollen-receptive stigmatic surface external to the outer integument. It is assumed here that those angiosperms with unitegmic ovules represent a secondary modification within the flowering plant clade.

Numerous mechanisms have been suggested for the enclosure of angiosperm ovules and the formation of a simple conduplicate carpel. In this paper the hypothesis is adopted that the carpel represents a "cupulate" megasporophyll such as occurs in *Caytonia* and corystosperms, perhaps modified by progenesis (Doyle, 1978).

9.35 Female gametophyte of 4–16 nuclei. In all seed plants where it is known, the female gametophyte is much more extensive than in angiosperms.

9.36 Double fertilization. The process of double fertilization in angiosperms that results in the formation of a zygote and endosperm nucleus does not occur in other seed plants. The closest approach to the angiosperm situation is in *Ephedra,* in which one of the male gametes fuses with the ventral canal nucleus of the archegonium, but this second zygote undergoes no further divisions (Moussel, 1978; Sporne, 1971a: 187).

9.37 Laminate endexine lacking. All gymnosperm pollen that has been studied in sufficient detail has a laminate endexine. In angiosperms the endexine is generally unlaminated except close to the apertures (Doyle et al., 1975), and some angiosperms appear to lack any endexinous layer (Walker, 1974a). Lugardon and LeThomas (1974) have suggested that the laminated endexine of gymnosperms is in fact homologous to the foot layer (innermost ektexine) of angiosperm pollen and that the endexine of angiosperms arose de novo (Zavada, 1984). If this interpretation is accepted, then the apparent endexinous laminations of some Annonaceae (Walker, 1976) and Trimeniaceae (Sampson & Endress, 1984) are not homologous to those of gymnosperms. Interpreting this complex character is difficult (Hill & Crane, 1982: 344–345) and requires further investigation aimed particularly at clarifying general patterns of pollen wall ontogeny.

TABLE 9. Data matrix for characters of seed plants: apomorphic characters marked +, plesiomorphic characters marked −, not applicable marked NA. Cladogram 1 (Fig. 20) was constructed from version one of the data in which Bennettitales and *Pentoxylon* were scored as plesiomorphic for characters 9.19 and 9.22; and character 9.25 was excluded as redundant. Cladogram 2 (Fig. 22) was constructed from version two of the data in which Bennettitales and *Pentoxylon* were scored apomorphic for characters 9.19, 9.22, and 9.25. See text for further discussion of these two alternatives.

Character	*Archaeopteris*	Medullosans	Cycads	*Lyginopteris*	*Cordaixylon*	*Mesoxylon*	*Lebachia*	Extant Conifers
1. Eustele	+	−	+	+	+	+	+	+
2. Embryogenesis with a free nuclear phase	−?	+?	+	+?	+?	+?	+?	+
3. Single functional megaspore mother-cell per megasporangium	−	+	+	+	+	+	+	+
4. Integument	−	+	+	+	+	+	+	+
5. Micropyle	NA	+	+	+	+	+	+	+
6. Linear tetrad of megaspores	−	+?	+	−	+?	+?	+?	+
7. Double vascular supply to ovules	NA	+	+	−	−	−	−	−
8. Axillary branching	−	+	−	+	+	+	+	+
9. Saccate pollen	NA	−	−	−	+	+	+	+
10. Flattened ovules	NA	−	−	−	+	+	+	+
11. Megaphyllous leaves organized on a pinnate plan	−	+	+	+	−	−	−	−
12. Narrowly triangular awl-shaped leaves	−	−	−	−	−	−	+	+
13. Megasporophylls borne on short fertile shoots in the axil of a bract or leaf	−	−	−	−	+	+	+	+
14. Fertile axillary ovulate shoots aggregated into an "inflorescence"	NA	NA	NA	NA	+	+	+	+
15. Pollen with distal germinal aperture	−	−	+	−	+	−	−	+
16. *Cordaites* foliage	−	−	−	−	+	+	−	−
17. Primary axis of ovulate and microsporangiate "inflorescences" dorsiventrally flattened with bracts and fertile shoots four-ranked	NA	NA	NA	NA	+	+	−	−
18. Siphonogamy	NA	−?	−	−?	−?	−?	−?	+
19. Ovules borne in a "cupule"	NA	−	−	−	−	−	−	−
20. Megaspore membrane thin	−	−	−	−	−	−	−	−
21. Granular pollen wall	+	−	−	+?	−	−	−	−
22. Uniovulate "cupule"	NA	NA	NA	NA	NA	NA	NA	NA
23. Microsporophylls forming "flowers"	−	−	−	−	−	−	−	−
24. Uniovulate "cupule" erect	NA	NA	NA	NA	NA	NA	NA	NA
25. Megasporophylls "unicupulate"	NA	NA	NA	−	NA	NA	NA	NA
26. "Unicupulate" megasporophylls aggregated to form heads	NA	NA	NA	NA	NA	NA	NA	NA
27. Male gametophyte of three or four nuclei	−?	−?	−	−?	−	−	−?	−
28. Female gametophyte tetrasporic	−	−?	−	−?	−?	−?	−?	−
29. Archegonia absent	−?	−	−	−	−	−?	−?	−
30. Embryo with "feeder"	−?	−?	−	−?	−?	−?	−?	−?
31. Ribbed pollen	−	−	−	−	−	−	−	−
32. Vessels with porose perforation plates	−	−	−	−	−	−	−	−
33. Microsporangiate and ovulate "flowers" with opposite pairs of bracteoles	NA	NA	NA	NA	NA	NA	NA	NA
34. Bitegmic ovule enclosed or partly enclosed by a structure with a pollen-receptive stigmatic surface external to the second integument	NA	NA	NA	NA	NA	NA	NA	NA

TABLE 9. Continued.

Ginkgo	*Callistophyton*	Peltasperms	Glossopterids	*Caytonia*	Corystosperms	Bennettitales	*Pentoxylon*	*Gnetum*	*Welwitschia*	*Ephedra*	Angiosperms
+	+	+?	+	+?	+	+	+	+	+	+	+
+	+?	+?	+?	+?	+?	+?	+?	+	−	+	−
+	+	+	+	+	+	+	+	+	+	+	+
+	+	+	+	+	+	+	+	+	+	+	+
+	+	+	+	+	+	+	+	+	+	+	+
+	+?	+?	+?	+?	+?	+	+?	NA	NA	+	+
−	−	−?	−	−	−?	−	−	−	−	−	−
+	+	+?	+	+	+?	+	+	+	+	+	+
−	+	−	+	+	+	−	−	−	−	−	−
+	+	+	+	+	+	+	+	−	−	+	−
−	+	+	+	+	+	+	+	+	−	−	+
−	−	−	−	−	−	−	−	−	−	−	−
+	−	−?	−?	−?	−?	−	−	−	−	−	−
NA	NA	NA?	NA?	NA?	NA?	NA	NA	NA	NA	NA	NA
+	+	+	+	+	+	+	+	+	+	+	+
−	−	−	−	−	−	−	−	−	−	−	−
NA	NA	NA?	NA?	NA?	NA?	NA	NA	−	−	−	NA
−	+	−?	−?	−?	−?	−?	−?	+	+	+	+
−	−	−	+	+	+	−/+	−/+	−	−	−	+
−	−	−	−	+	+	+	+	+	+	+	+
−	−	−	−	−	+	+	+	+	+	+	+
NA	NA	NA	−	−	+	−/+	−/+	NA	NA	NA	+
−	−	−?	−?	−?	−?	+	+	−	+	+	+
NA	NA	−	−	−	−	+	+	NA	NA	NA	−
NA	NA	−	−	−	−	−/+	−/+	NA	NA	NA	−
NA	NA	NA	NA	NA	NA	+	+	NA	NA	NA	NA
−	−	−?	−?	−?	−?	−?	−?	+	+	−	+
−	−?	−?	−?	−?	−?	−	−?	+	+	−	−
−	−	−?	−	−?	−?	−?	−?	+	+	−	−
−	−	−?	−?	−?	−?	−	−?	+	+	−	−
−	−	−	−	−	−	−	−	−	+	+	−
−	−	−?	−	−?	−	−	−	+	+	+	−
NA	NA	NA?	NA?	NA?	NA?	−	−	+	+	+	−
NA	NA	NA	NA	NA	−	−	−	NA	NA	NA	+

TABLE 9. Continued.

Character	*Archae-opteris*	Medul-losans	Cycads	*Lygin-opte-ris*	*Cor-daixy-lon*	*Mes-oxylon*	*Le-bach-ia*	Ex-tant Coni-fers
35. Female gametophyte of four to 16 nuclei	−?	−	−	−	−	−?	−?	−
36. Double fertilization	−?	−?	−	−?	−?	−?	−?	−
37. Laminate endexine lacking	−?	−	−	−?	−?	−?	−?	−
38. Axially aligned companion cells derived ontogentically from the same mother-cells as the sieve elements	−?	−?	−	−?	−?	−?	−?	−

9.38 Axially aligned companion cells derived ontogenetically from the same mother-cells as the sieve elements. This character apparently occurs only in angiosperms and is not known in any other group of seed plants (Hill & Crane, 1982).

CLADOGRAMS

Cladograms were generated from the data matrix using the PAUP Program (Phylogenetic Analysis Using Parsimony) of D. L. Swofford with the global branch swapping and MULPARS option. Cladograms were rooted by incorporation of a hypothetical ancestor scored as plesiomorphic for all characters. Two different forms of the matrix (Table 9) were used to generate two different cladograms as follows.

Cladogram 1 (Fig. 20). Cladogram 1 was generated from version one of the data matrix in which the "cupules" of Bennettitales and *Pentoxylon* were not coded as homologous to the "cupules" of glossopterids, *Caytonia,* corystosperms, and angiosperms. That is, Bennettitales and *Pentoxylon* were coded as plesiomorphic for characters 9.19 and 9.22. Character 9.25 was excluded as redundant (coded by character 9.24) giving in a total of 37 characters. The analysis resulted in five equally parsimonious cladograms (61 character state transitions) all with very similar topologies. A strict consensus tree (Rohlf, 1982) derived from those five cladograms is given in Figure 20. This kind of consensus tree preserves only those aspects of tree topology that occur in the five original trees. In this case the consensus tree only resulted in one polychotomy.

Cladogram 2 (Fig. 22). Cladogram 2 was generated from version two of the data matrix in which the "cupules" of Bennettitales were coded as homologous to those of glossopterids, *Caytonia,* corystosperms, and angiosperms. That is, Bennettitales and *Pentoxylon* were coded as apomorphic for characters 9.19, 9.22, 9.24, 9.25, giving a total of 38 characters. The analysis resulted in ten equally parsimonious cladograms (62 character state transitions) all with very similar topologies. A strict consensus tree derived from these ten cladograms is given in Figure 22.

DISCUSSION AND INTERPRETATION (GYMNOSPERMS)

The pattern of relationships in cladograms 1 and 2 is very similar. In both, seed plants are interpreted as a monophyletic group defined by the presence of an integument (character 9.4) with a well-differentiated micropyle (character 9.5) surrounding a megasporangium with a single functional megaspore mother-cell (character 9.3) and having a free nuclear phase in embryogenesis (character 9.2, secondarily cellular in *Welwitschia* and angiosperms). The possibility of seed plant polyphyly suggested by Arnold (1948), Beck (1981), and Chaloner et al. (1977) is not supported by the cladogram, but a full analysis of this problem would have to take into account additional progymnosperms and primitive seed plants that currently are only poorly known.

Lyginopteris is resolved by both cladograms as the sister taxon to all other seed plants considered. However, the characters on which this division is based are not strong. Distal pollen aperture (character 9.15) is particularly problematic (see below), and although *Lyginopteris* probably had a tetrahedral tetrad of megaspores, the distributrion of tetrahedral and linear tetrads in other fossil plants is not well known.

A close relationship between the Carboniferous pteridosperms and cycads has been recognized by many authors. Arnold (1953) and Scott (1923) suggested that cycads were closely related

TABLE 9. Continued.

Ginkgo	*Callistophyton*	Peltasperms	Glossopterids	*Caytonia*	Corystosperms	Bennettitales	*Pentoxylon*	*Gnetum*	*Welwitschia*	*Ephedra*	Angiosperms
–	–	–?	–	–?	–?	–?	–?	–	–	–	+
–	–?	–?	–?	–?	–?	–?	–?	–	–	–	+
–	–?	–?	–?	–?	–?	–?	–?	–	–	–	+
–	–?	–?	–?	–?	–?	–?	–?	–	–	–	+

to lyginopterid pteridosperms, while Delevoryas (1955), Stewart (1983), and Wordsell (1906) have favored a closer, even ancestor-descendant, relationship from medullosans. Cladogram 1 supports the view that medullosans and cycads are sister taxa based on the double vascular system in the ovule (character 9.7). This assumes that the *Lagenostoma* cupule has no homology in the cycad ovule, and that the chalazal pad of vascular tissue in the ovules of conifers, cordaites (*Cordaixylon, Mesoxylon*), and *Callistophyton* is not the remains of a previous inner integument (see character 9.7). In cladogram 2 the position of cycads and medullosans relative to each other, and relative to all other seed plants considered (except *Lyginopteris*), is not resolved. Both cladograms suggest that the apparent absence of axillary branching in cycads (character 9.8) is the result of secondary loss, and that axillary branching is a potential seed plant synapomorphy. Loss of axillary branching may be one result of the specialized pachycaul habit of extant cycads. The relationships of *Spermopteris, Phasmatocycas,* and *Archaeocycas* to cycads (Mamay, 1976) are discussed later in this paper. Similarly, both cladograms suggest that the protostele of *Quaestora* is reduced from the eustele that characterizes all other seed plants considered. This conclusion may have to be modified if it could be demonstrated that cycads and medullosans were closely related to aneurophytalean progymnosperms (protostelic) as suggested by some authors (e.g., Stewart, 1983).

The evidence for a close relationship between conifers and cordaites was presented convincingly by Florin (1951) and has been accepted widely by subsequent authors (Mapes & Rothwell, 1984; Rothwell, 1982b). Recently, however, Beck (1981: 193) has suggested "that the Cordaitales and Lebachiaceae represent independent lines of evolution originating from *Archaeopteris* or some closely related, similar progymnosperm." This hypothesis would require at least a biphyletic origin of seed plants that is not supported by the analyses in this paper. The cladograms reflect the views of Florin and other authors. They suggest that conifers and cordaites are more closely related to each other than either is to *Archaeopteris* on the basis of several derived characters: single functional megaspore mother-cell per megasporangium (character 9.3), integument (character 9.4), micropyle (character 9.5), axillary branching (character 9.8), saccate pollen (character 9.9), flattened ovules (character 9.10), megasporophylls borne on short fertile shoots in the axils of bracts (character 9.13), and ovulate short shoots aggregated into an "inflorescence" (character 9.14). Rothwell (1982b) has similarly emphasized the importance of these characters in his analysis of Beck's hypothesis. The microsporangiate "inflorescence" of *Cordaites* is a feature that has been suggested as a specialization precluding an ancestral relationship to the conifers (Beck, 1981; Pant, 1977b). In cladistic terms this character would be a synapomorphy of cordaites but would not obviate a close relationship with conifers. The difficulty only arises when the relationship between the two groups is viewed as that of an ancestor and descendant. Similar arguments could be applied to other, possibly unique, specializations of cordaites listed by Beck (1981: 215) (leaf morphology, bilaterally symmetrical distichous inflorescences).

The closest relatives of *Ginkgo* have long been thought to be conifers and cordaites (Chamberlain, 1935; Emberger, 1954; Pant, 1977b), and this is supported by both cladograms in which *Ginkgo* is placed as the sister taxon to the conifer

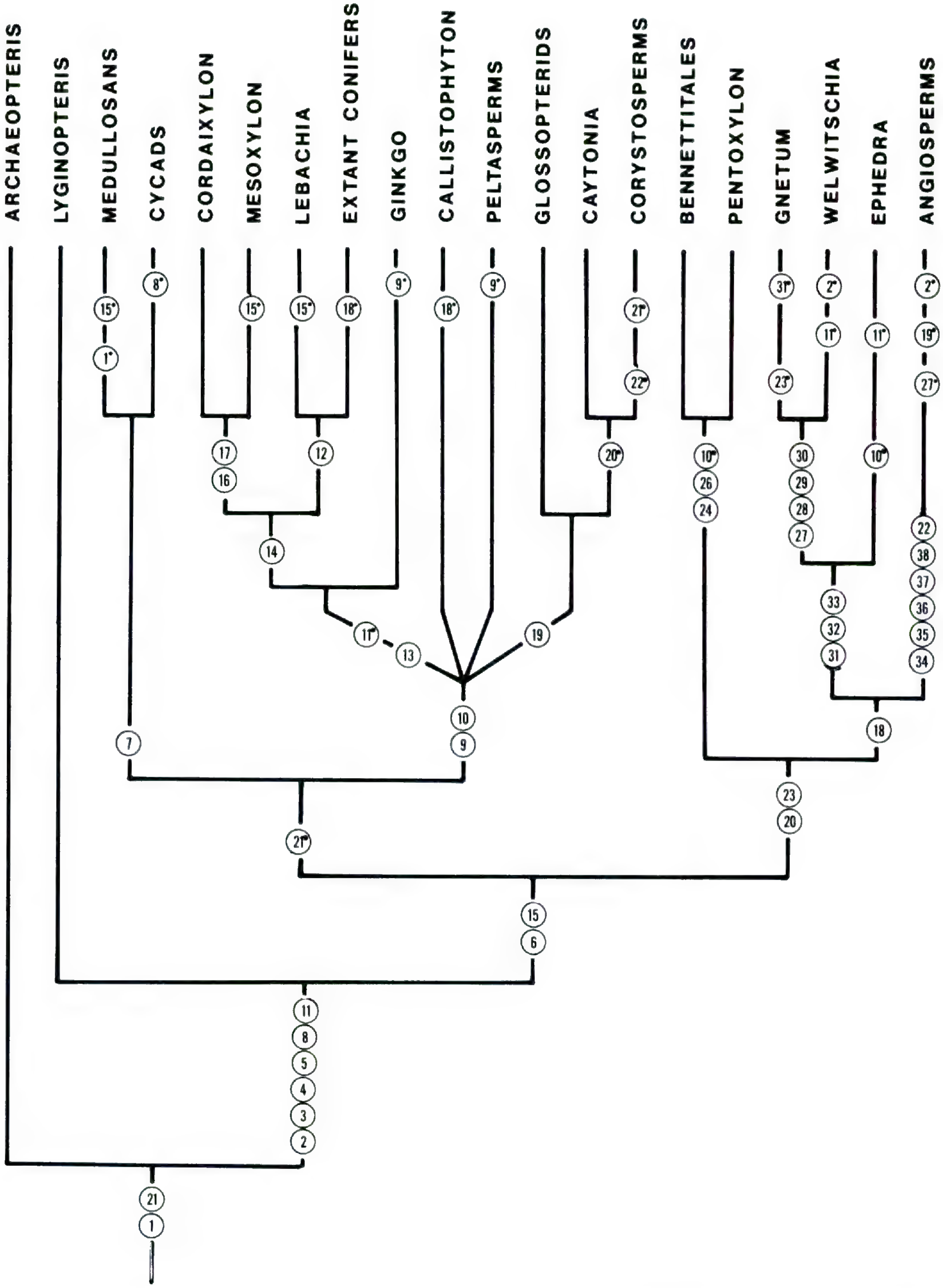


FIGURE 20. Relationships beween major groups of seed plants. Strict consensus tree derived from five equally parsimonious cladograms constructed from version one of the data matrix. In this analysis the "cupules" of Bennettitales and *Pentoxylon* were not coded as homologous to the "cupules" of glossopterids, *Caytonia,* corystosperms, and angiosperms. Bennettitales and *Pentoxylon* were coded as plesiomorphic for characters 9.19 and 9.22, and character 9.25 was excluded as redundant. Total characters 37, character state transitions 61. A dot next to the number indicates homoplasy.

plus the cordaite clade. The synapomorphy of the *Ginkgo* plus conifer plus cordaite clade is the presence of megasporophylls on an axillary fertile shoot (character 9.13). The morphological interpretation presented earlier (p. 749) of the *Ginkgo* ovulate reproductive structure is therefore critical. There is no support in the analysis of characters presented here for Meyen's (1984) view that *Ginkgo* and related plants constitute a very distinct major lineage in seed plant evolution. *Ginkgo* is resolved as more closely related to conifers and cordaites than to any of the taxa included by Meyen in his Ginkgoopsida. Similarly, although *Ginkgo* shares some features such as zooidogamy and the long free nuclear phase of embryogenesis with the living cycads (Stewart, 1983: 319), in cladistic terms these are primitive characters that do not indicate close phylogenetic relationship (Chamberlain, 1935: 216).

Rothwell (1981) discussed two possibilities for the phylogenetic relationships of *Callistophyton*: either it is more closely related to conifers and cordaites than it is to other pteridosperms, or the similarities with conifers and cordaites are because of parallel evolution. He rejected both and suggested a position intermediate between pteridosperms and cordaites or conifers. Both cladograms reflect the difficulties in resolving the precise phylogenetic relationship of *Callistophyton* and have a polychotomy involving cordaites plus conifers, *Callistophyton,* peltasperms, and the glossopterid plus *Caytonia* plus corystosperm clade. These four groups are themselves united by flattened seeds (character 9.10) and saccate pollen (lost secondarily in peltasperms, character 9.9).

One advanced character that may ultimately be important in assessing the relationships of *Callistophyton* is the presence of pollen with a distal aperture. In both cladograms it is methodologically more parsimonious to interpret the proximal germinal apertures in medullosans, *Mesoxylon,* and *Lebachia* as reversals from distal germination primitive for all seed plants except *Lyginopteris* (a total of three reversals). However, from a botanical perspective such reversals seem unlikely and most paleobotanists would probably view the prepollen of medullosans, *Mesoxylon,* and *Lebachia* as retention of a primitive feature. If this view is adopted it necessitates five (cladogram 2) or six (cladogram 1) independent origins of distal germination. Chaloner (1970a) recognized that the switch from proximal to distal germination had occurred several times in seed plant evolution, but the extent of this parallelism is of considerable interest. It suggests that detailed studies of pollen ontogeny might detect different mechanisms of aperture formation, and it clearly indicates that pollen with a distal aperture is not a good synapomorphy of seed plants as might be concluded from a cladistic analysis restricted solely to extant gymnosperms.

At the same level as *Callistophyton* in the cladogram the systematic relationships of peltasperms are unresolved; but the other group incorporated at this polychotomy is the glossopterid plus *Caytonia* plus corystosperm clade defined by the presence of a "cupule" (character 9.19). Within this group *Caytonia* and corystosperms are more closely related to each other than either is to glossopterids based on the poorly developed acid-resistant megaspore membrane (character 9.20). These relationships among "Mesozoic seed ferns" are maintained in both cladograms.

The relationships of *Pentoxylon* previously have been considered enigmatic. Frequently the genus has been viewed as a peculiar and isolated gymnosperm of uncertain phylogenetic relationship (Andrews, 1961; Stewart, 1983) though various similarities with other groups of seed plants have been pointed out. For example, monosulcate pollen occurs in cycads, *Ginkgo,* and the Bennettitales, while pycnoxylic conifer-like wood is a generalized feature within seed plants as a whole. Other authors (e.g., Ehrendorfer, 1971) have suggested a close relationship between *Pentoxylon* and the Bennettitales. In the analysis given here two relatively advanced characters are useful in establishing the phylogenetic relationships of *Pentoxylon*: the "flower-like" arrangement of the microsporophylls (character 9.23), which also occurs in Bennettitales, Gnetales, and angiosperms; the aggregation of the ovules into a head (character 9.26), which otherwise occurs only in the Bennettitales, and the structural similarity of bitegmic bennettitalean and *Pentoxylon* ovules (characters 9.19, 9.25, 9.26). If the interseminal scales of Bennettitales are accepted as being derived ontogenetically and phylogenetically from "cupule" primordia (characters 6.1, 9.19) then the existence of fully fertile ovulate heads like those of *Pentoxylon,* which lack interseminal scales, is a straightforward and reasonable prediction. This general view (though before *Pentoxylon* had been studied) was expressed by Wieland (1906: 120). The stomata of

Nipaniophyllum (*Pentoxylon*) were originally described by Sahni (1948: 56) as syndetocheilic, and they deserve careful reexamination to clarify the range of variation which they exhibit and to establish their precise similarities and differences with those of the Bennettitales. It is also interesting that the anticlinal flanges of *Nipaniophyllum* leaf cuticles are finely sinuous, like those of most Bennettitales.

A close relationship between Bennettitales and cycads is not supported by the cladogram, although the two groups frequently have been treated together on the basis of their leaf morphology and the similar habit of cycads and *Cycadeoidea* (Wieland, 1906, 1916). Both cladograms suggest that these similarities are the result of convergence. Many authors (Arber & Parkin, 1907: 51; Arnold, 1953: 58; Stewart, 1983) have recognized that the cycad plus Bennettitales group is artificial and probably does not reflect close phylogenetic relationship. The two groups are treated together primarily for reasons of convenience and tradition, but according to the analysis in this paper even the general designation of the Bennettitales as "cycadophytes" obscures their probable phylogenetic relationships with other taxa. On the basis of the characters given here, the two groups are very far apart.

In both cladograms the Bennettitales plus *Pentoxylon* clade is resolved as a sister group to a clade comprising the angiosperms plus Gnetales exactly as proposed by Arber and Parkin (1908). The probability of a close relationship between the Bennettitales and Gnetales frequently has been suggested (Arber & Parkin, 1907, 1908; Martens, 1971: 269; Takhtajan, 1969: 17; Thoday, 1911), but at this level of analysis the cladogram does not support the view that the gnetalean "flower" is a highly reduced bisexual bennettitalean "flower" consisting of a single ovule or that the Gnetales and Bennettitales are sister taxa. It is nevertheless possible that a more detailed character analysis might place the Gnetales as a relatively advanced monophyletic group within the bennettitalean clade. If this could be supported then a bennettitalean origin for the gnetalean "flower" would be more plausible. In this case the bennettitalean "perianth" (character 9.33) may be interpreted as homologous to the opposite bracteoles of the Gnetales, and the "slight protruberance slightly below the epicotyl" in *Cycadeoidea* embryos (Crepet, 1974: 158) could be compared to a poorly developed "feeder" in *Welwitschia* or *Gnetum* (character 9.30). Other similarities between the Bennettitales and Gnetales include the details of the micropyle and seeds (Berridge, 1911; Thoday, 1911), paracytic stomata, bisporangiate flowers, the possible presence of vessels (Krassilov, 1984), and the presence of a long micropylar tube. Cladogram 2 also supports the view that the apparent absence of a true outer integument in Gnetales is most easily explained as a secondary loss.

The main alternative to a bennettitalean or angiosperm relationship of the Gnetales is the possibility of a close relationship between *Ephedra* and cordaites (Eames, 1952). Eames emphasized the difference between *Ephedra* versus *Gnetum* and *Welwitschia*. The cladogram supports the view that *Gnetum* and *Welwitschia* are more closely related to each other than either is to *Ephedra* based on the reduced male gametophyte (character 9.27), the tetrasporic female gametophyte (character 9.28), the lack of archegonia (character 9.29), and the presence of a "feeder" in the embryo (character 9.30; see also p. 766). However, contrary to Eames (1952) the cladogram suggests that the Gnetales are monophyletic and united by fundamentally similar reproductive structures (character 9.33), vessels (character 9.32), and possibly by their distinctive, ribbed pollen (character 9.31). Eames based his discussion mainly on the fertile axillary shoot that occurs in both Gnetales and cordaites, and his views hinge in particular on an interpretation of the ovules in *Ephedra* as appendicular rather than cauline. The other *Ephedra*-cordaite similarities cited by Eames (1952) are interpreted here as primitive features within seed plants (pycnoxylic wood, anomocytic stomata) or independently derived in the spermatophyte clade (non-megaphyllous leaves).

In most features already discussed cladograms 1 and 2 scarcely differ, but the most prominent and almost the sole effect of interpreting the other integument of Bennettitales and *Pentoxylon* as homologous with the "cupule" in glossopterids, *Caytonia*, corystosperms, and angiosperms is to reposition the Bennettitales plus *Pentoxylon* plus Gnetales plus angiosperm clade as the sister group to the corystosperms. Under this interpretation the orthotropous bitegmic ovules of Bennettitales and *Pentoxylon* may be considered the ultimate product of a reduction series involving the *Caytonia* megasporophyll with several "cupules" and several seeds in each; and the corystosperm megasporophyll with fewer "cupules" each containing a single seed. The bennettitalean

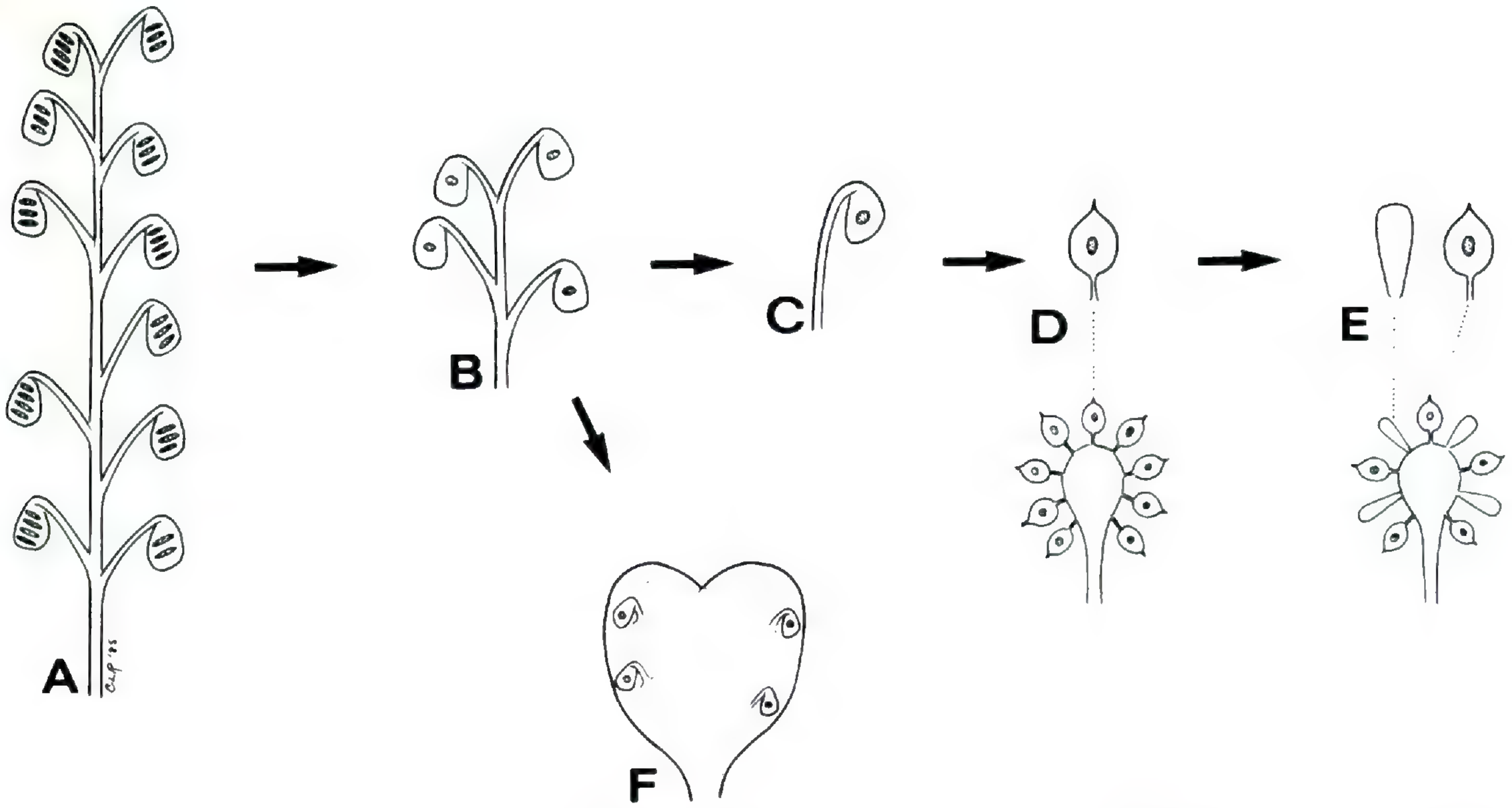


FIGURE 21. Suggested homologies between megasporophylls of *Caytonia,* corystosperms, *Pentoxylon,* Bennettitales, and angiosperms.—A. *Caytonia*-like megasporophyll with several "cupules," each containing numerous ovules.—B. Corystosperm-like megasporophyll with few uniovulate "cupules."—C. Hypothetical recurved "unicupulate" megasporophyll containing one ovule.—D. Erect ("orthotropous") "unicupulate" megasporophylls containing a single ovule, aggregated into a head as in *Pentoxylon.*—E. Head of fertile and sterile "unicupulate," uniovulate megasporophylls as in Bennettitales. Sterile megasporophylls forming interseminal scales.—F. Angiosperm carpel opened and viewed adaxially. See text for further explanation.

or *Pentoxylon* ovule would be interpreted as a highly reduced megasporophyll of one "cupule" containing a single seed (Fig. 21, see also Thomas, 1955: 655). In my view the only major argument against this interpretation is the orthotropous orientation of bennettitalean and *Pentoxylon* "cupules" versus the recurved "cupules" of *Caytonia* and corystosperms. Clearly it would be of considerable interest if the predicted (but unknown) recurved bitegmic ovules were detected in primitive Bennettitales.

In favor of the relationship suggested in cladogram 2 is the similarity of ovule structure and cuticles in *Caytonia,* corystosperms, Bennettitales, and *Pentoxylon.* Additional evidence is provided by the similarity between *Rhexoxylon* (probable corystosperm stem) and *Pentoxylon.* Both have a "polystelic" arrangement of vascular tissue and also show an identical pattern of leaf-trace origin (Stewart, 1983: 312). On the basis of this slim evidence I currently favor cladogram 2 over cladogram 1 as most likely approaching the true phylogenetic relationships of seed plants, and this view is also more broadly consistent with the stratigraphic evidence. Cladogram 1 places the origin of four fundamentally Mesozoic groups (Bennettitales, *Pentoxylon,* Gnetales, and angiosperms) at a level equivalent to the origin of major Paleozoic groups such as medullosans and cordaites. Further work is clearly necessary to supplement our knowledge of characters and plants relevant to the competing hypotheses of cladograms 1 and 2. In particular, a detailed comparative study of the "cupules" of *Vardekloeftia* (Harris, 1932b), *Bennetticarpus crossospermus* (Harris, 1932b), other Bennettitales (Stopes, 1918; Wieland, 1906: 120; Kräusel, 1949), *Pentoxylon,* and corystosperms is a primary requirement.

In addition to the particular questions of relationship already considered, the cladograms raise two general issues: are the pteridosperms a phylogenetically useful group, and how well do existing classifications of seed plants reflect phylogenetic relationships? The extreme heterogeneity of the "pteridosperms" is clearly demonstrated in both cladograms. The relationships of medullosans, *Lyginopteris, Callistophyton,* peltasperms, glossopterids, *Caytonia,* and corystosperms are extremely diverse, and there is no pair of pteridosperm taxa that together constitute a monophyletic group in both cladograms. Generally the concept of the pteridosperms has been used intuitively with little attempt at rigorous

TABLE 10. Previous classification of gymnosperms. Extinct taxa indicated with an asterisk.

Chamberlain, 1935	*Bierhorst, 1971*
Cycadophytes	Cycadopsida
*Cycadofilicales	*Pteridospermales
*Bennettitales	Cycadales
Cycadales	*Cycadeoidales
Coniferophytes	*Caytoniales
*Cordaitales	Coniferopsida
Ginkgoales	*Cordaitales
Coniferales	Coniferales
Gnetales	Taxales
	Ginkgoales
	Gnetopsida
	Ephedrales
	Gnetales
	Welwitschiales
	Angiospermopsida

definition. However, Townrow (1962a: 316) offered a more precise circumscription defining the pteridosperms as "gymnospermous plants with leaves, pollen- and seed-bearing organs pinnate. Reproductive structures not aggregated into cones or flowers." This defines the pteridosperms entirely in terms of pinnately organized leaves, microsporophylls, and megasporophylls (character 9.11), which are all generalized features within most groups of seed plants. On this definition the pteridosperms are merely the residue of seed plants after taxa with "cones" (cycads, conifers, cordaites, *Pentoxylon*) and taxa with "flowers" (presumably Bennettitales, Gnetales, and angiosperms) have been removed. The group is defined by exclusion and primitive characters. For phylogenetic purposes the current concept of the pteridosperms is valueless and has been a major source of confusion in attempts to analyze the phylogenetic relationships of seed plants.

The pattern of relationships expressed in the cladogram can be usefully compared with views expressed in the classifications of previous authors. It should, however, be recognized that classifications may be viewed as having many purposes, and not all were intended to reflect phylogenetic relationships. Considering only extant gymnosperms the cladogram compares favorably with the classification of Chamberlain (1935) (Table 10). Chamberlain divided the extant gymnosperms into two groups, cycadophytes, in which he placed the cycads, and coniferophytes, in which he included the conifers, *Ginkgo,* and Gnetales. He clearly recognized the distinctiveness of the cycads, and that the conifers, *Ginkgo* and Gnetales were more closely related. Bierhorst (1971) (Table 10) separated the Gnetopsida from the Coniferopsida, although he acknowledged that they are probably more closely related than either is to cycads. However, when the comparisons are extended to include fossil plants, the cladogram conflicts with the classifications of Chamberlain (1935) and Bierhorst (1971). Both these authors recognized the Pteridospermales (Cycadofilicales) and the Cycadeoidales (Bennettitales) as two groups within the Cycadopsida (Cycadophytes). The heterogeneity of the pteridosperms already has been discussed, and according to cladogram 1, conifers, cordaites, and *Ginkgo* are more closely related to cycads than to Bennettitales. In cladogram 2 the Bennettitales are more closely related to conifers, cordaites, *Ginkgo,* and Gnetales. Bierhorst (1971) also included *Caytonia* in the Cycadopsida. In both cladograms *Caytonia* is more closely related to conifers, cordaites, and *Ginkgo.* The results presented here suggest that in order for the cycadophytes to be considered a monophyletic group, it should probably include only the medullosans and cycads.

If the cycadophytes of Chamberlain's system are redefined in restricted form, the "coniferophytes" according to both cladograms expand to include *Callistophyton,* glossopterids, *Caytonia,* and corystosperms. In cladogram 2 the Bennettitales, *Pentoxylon,* Gnetales, and angiosperms are also included in the coniferophyte clade. In this context many of the traditional distinctions between the cycadophytes and coniferophytes break down, and the "coniferophytes" no longer include only forms with profuse branching, small simple leaves, small pith and cortex, and pycnoxylic secondary xylem (Foster & Gifford, 1974: 385). If the relationships in cladogram 2 are accepted, it may be more useful to recognize a broad group ("platysperms") defined by the presence of flattened ovules. Radiospermic ovules has been one of the characters traditionally used to link the cycads with the Bennettitales and even has been used to suggest a relationship between the Gnetales and medullosans (Rodin & Kapil, 1969: 429). Under the interpretation in cladogram 2, the Bennettitales and Gnetales are only secondarily radiospermic, and some, such as *Vardekloeftia* and *Ephedra,* are platyspermic. There is, in any case, very little resemblance between the small, poorly vascularized ovules of the Bennettitales and the large, doubly vascularized ovules of cycads. According to the analysis of characters

in this paper, the radiospermy of cycads, medullosans, and *Lyginopteris* is not homologous with the secondary "pseudoradiospermy" of Bennettitales and Gnetales.

DISCUSSION AND INTERPRETATION (ANGIOSPERMS)

The angiosperms along with the Gnetales and the Bennettitales plus *Pentoxylon* clade form a monophyletic group. In cladogram 1 this clade is placed as the sister group to all other seed plants considered (except *Lyginopteris*). In cladogram 2 the corystosperms are the sister group to the Bennettitales plus *Pentoxylon* plus Gnetales plus angiosperm clade. This second pattern of relationships is broadly consistent with the view that the "Mesozoic seed ferns" were important in angiosperm origins (Andrews, 1961; Doyle, 1978; Gaussen, 1946; Retallack & Dilcher, 1981; Stebbins, 1974; Stewart, 1983) and reconciles this idea with the suggestions of Arber and Parkin (1907, 1908) concerning the relationships of angiosperms to the Gnetales and Bennettitales.

The analysis of characters presented here does not address the possibility that the angiosperms are polyphyletic (Hughes, 1976, 1977; Krassilov, 1973, 1975; Meeuse, 1966) and accepts the traditional view that the angiosperms are monophyletic (Cronquist, 1968; Takhtajan, 1969). In cladistic terms polyphyly could only be supported if a group of flowering plants could be shown to be more closely related to some group of gymnosperms than to other flowering plants. This has never been explicitly demonstrated, but is implicit in Krassilov's (1977b) suggestion that there are three major mid-Cretaceous angiosperm "lineages," the Hamamelidales, Laurales, and monocotyledons, that are "rooted" in the Dirhopalostachyaceae, Caytoniales, and Czekanowskiales, respectively. In both cladograms the angiosperms could be justified as monophyletic by five characters (9.34–9.38; see also Hill & Crane, 1982). It should, however, be recognized that most of these features are difficult to assess even in living plants, that most species in the Magnoliidae are relatively poorly understood, and that there are real problems of sampling in such a large group.

An interesting aspect of the cladogram is that the flowering plants are more closely related to Gnetales than any other group of gymnosperms. This view was advocated in the earlier part of this century (Arber & Parkin, 1908) but has been out of favor for over 50 years, apparently for two principal reasons. The first is the apparent difficulty of "transforming" the ovulate structures of the Gnetales into an angiosperm carpel. Although this has been attempted by several authors (Meeuse, 1966; Thompson, 1916), the results have been unconvincing and usually have involved comparison with the ovary in some "Amentiferae" that are more likely to represent secondary modifications within the flowering plant clade. These hypotheses also have been unable to account for the origin of the conduplicate carpel.

The second reason stems from the widely accepted view that vessels arose independently in the Gnetales and angiosperms (see earlier discussion of characters 1.6, 9.32). This view has been so influential that, even when the many similarities between Gnetales and angiosperms have been acknowledged, the conclusion has been that "the evidence of vascular anatomy strongly controverts any suggestion of relationships" (Cronquist, 1968: 43).

Both of these problems seem to arise out of the preoccupation with identifying angiosperm ancestors and the apparent impossibility that the Gnetales could have fulfilled this role. From a cladistic standpoint, such an ancestor-descendant relationship is untenable; some of the similarities between the two groups indicate a close phylogenetic relationship, but each has its own specializations with neither being ancestral to the other (see also Arber & Parkin, 1908; Just, 1948). Interestingly too, several of the gnetalean features that appear to be present in flowering plants (e.g., the dicotyledonous leaves of *Gnetum*) may well be secondary advances *within* the gnetalean clade.

In both cladograms, the Gnetales and angiosperms are resolved as sister groups (cf. Arber & Parkin, 1908; Just, 1948) but exhibit some parallelisms. Angiosperms share several derived features with *Gnetum* and *Welwitschia,* including the poorly developed male gametophyte (character 9.27), embryogenesis with no free nuclear phase (character 9.2), precocious differentiation of integuments at the time of megasporogenesis (Crepet, 1974: 163), presence of astrosclereids (Bierhorst, 1971: 475), and the occurrence of paracytic stomata that, according to Baranova (1972), are primitive within angiosperms. In addition, angiosperms and *Gnetum* are similar in leaf morphology and in having a

partially (*Gnetum*) or completely coenocytic (angiosperms) female gametophyte at fertilization. Further similarities between the Gnetales and angiosperms, that require more detailed examination, are similarities in chemistry (Gottlieb & Kubitzki, 1984) particularly of the wood (Gibbs, 1958; McLean & Evans, 1934; Melvin & Stewart, 1969; Nishio, 1959), the occurrence of laticifers (Muhammad & Sattler, 1982), the small chromosomes, and the occurrence of polyploidy in *Ephedra* (Ehrendorfer, 1976). Ehrendorfer estimates the base chromosome number of Gnetales as $n = 7$, the same value as that estimated for the base number of angiosperms (Raven, 1975).

Arber and Parkin (1908: 513) explicitly recognized a sister-group relationship between the angiosperms and Gnetales, with the Bennettitales as a sister group to both. The Bennettitales were an important factor in the development of the Anthostrobilus theory of the angiosperm flower (Arber & Parkin, 1907) and were part of the justification for considering the "Ranalian plexus" as the most primitive living flowering plants. The cladogram provides an explicit base from which to examine further the idea that the Bennettitales, like *Pentoxylon* and Gnetales, are closely related to flowering plants and from which to pursue the functional parallelisms in terms of pollination and dispersal biology that can be traced in these clades.

Other hypotheses for the origin of the angiosperms are not supported by the distribution of characters in the cladogram. The cupules of lyginopterid seed ferns are not treated as homologous with those of "Mesozoic seed ferns" (character 9.19) and the cladogram lends no a posteriori support to this idea. Lyginopterid cupules therefore seem unlikely to be helpful in any parsimonious explanation of the origin of the second integument or carpel in angiosperms (Long, 1966, 1977). Indeed, results from a PAUP analysis of Table 9 in which the cupule of *Lyginopteris* is scored as homologous with the "cupules" of glossopterids, *Caytonia,* and corystosperms and the second integument of Bennettitales, *Pentoxylon* and angiosperms, place *Lyginopteris* in various highly derived positions inconsistent with other aspects of its morphology (and stratigraphic position). The suggestion that the carpel evolved by inrolling of a cycad-like megasporophyll (Mamay, 1976) is also unsupported by the relative positions of cycads and angiosperms in the cladogram. Inrolling of a simple megasporophyll would, in any case, only produce a carpel containing unitegmic ovules. Additionally, some of the plants (*Spermopteris, Phasmatocycas*) on which this hypothesis is based are interpreted here as platyspermic, and possibly more closely related to *Callistophyton,* the Mesozoic seed ferns, Bennettitales, Gnetales, and angiosperms, rather than to cycads (see below).

Similarly, the notion that the angiosperms are cycadopsid seed plants (Doyle, 1978; Stewart, 1983) is not supported by the cladogram. This idea can be traced to the view that the seed ferns are uniformly a cycadopsid group. In fact, the accretionary historical development of the seed-fern concept, and their original designation as "Cycadofilicales," has obscured their phylogenetic heterogeneity. In my view the seed ferns include both cycadopsid and coniferopsid forms (p. 776), and it is the latter taxa that are more closely related to angiosperms.

PHYLOGENETIC RELATIONSHIPS OF OTHER FOSSIL GYMNOSPERMS

EREMOPTERIS, NYSTROEMIA, AND SIMILAR PLANTS

Leaves, seeds, and probable microsporangia of *Eremopteris* were described by Delevoryas and Taylor (1969) from the Upper Pennsylvanian of Pennsylvania. The bipinnate leaves were closely associated with stalked flattened ovules. Each ovule possessed a pair of prominent apical "horns" and some showed probable well-developed megaspore membranes. Ovules and microsporangia of *Nystroemia pectiniformis* from the Permian of China (Halle, 1929) are similar to those of *Eremopteris.* Although important details of both *Eremopteris* and *Nystroemia* are unknown, the flattened ovules, combined with the lack of a "cupule" or conifer-cordaite-like inflorescence, suggests a combination of relatively advanced and primitive features similar to that seen in *Callistophyton* and peltasperms.

Permian pinnately organized leaves bearing ovules on the lamina or at the margin have been described as "callipteroid" (Mamay & Watt, 1971). *Tinsleya* (Mamay, 1966), *Sphenopteris tenuis* (Halle, 1929), *Emplectopteris triangularis* (Halle, 1929), and *Archaeocycas* (Mamay, 1976) are too poorly understood for detailed evaluation of their systematic relationships. It is, however, of interest that microsporophylls thought to be associated with these callipterid plants produced bisaccate pollen (see Mamay, 1966: 1).

SPERMOPTERIS, PHASMATOCYCAS, SOBERHEIMIA

Spermopteris coriacea (Goeppert) Cridland & Morris (1960) from the Upper Pennsylvanian of Kansas consists of entire-margined taeniopterid leaves bearing ovules on the abaxial surface. The ovules are confined to the distal portions of the leaf and form a row on either side of the midvein. They were oriented at right angles to the midvein with their micropyles arranged approximately along the margin. They were probably flattened with a distinct micropylar notch.

Phasmatocycas kansana Mamay (1976) is a megasporophyll with sessile ovules borne in two lateral rows. Distally the megasporophyll may have expanded into a lamina with taeniopterid venation (Mamay, 1976, but see Kerp, 1983). The ovules were flattened (Stewart, 1983: 283), had a shallowly bifid, notched apex similar to those of *Spermopteris,* a blunt, funnel-shaped micropyle, and a thick megaspore membrane. Recently collected material from Kansas (Pfefferkorn, pers. comm.) also has flattened ovules.

Soberheimia jonkeri Kerp (1983) from the Permian of Germany is similar to *Spermopteris* and *Phasmatocycas.* It is a leaf-like, bilaterally symmetrical structure with two rows of lateral organs interpreted as seeds. The lamina is thought to have been lobed with expansions between the seeds.

Mamay (1976) interpreted *Spermopteris* and *Phasmatocycas* as important plants in the evolution of cycads. According to the analysis of characters given here, a close relationship to cycads is unlikely. Cycads and medullosans do not have platyspermic seeds and, as in *Eremopteris* and *Nystroemia,* the possession of this feature, combined with the lack of a conifer-cordaite-like inflorescence or "cupules," is a combination of advanced and primitive features similar to that in *Callistophyton* and peltasperms.

VOJNOVSKYALES

The Vojnovskyales are a group of Permian plants described from Asia, North and South America, and Africa (Krassilov & Burago, 1981). Leaves of *Vojnovskya* (*Nephrolepis*) are fan-shaped and resemble those of the enigmatic Triassic plant *Sanmiguelia* (Ash, 1982; Becker, 1972; Tidwell et al., 1977) in the plications of the lamina and the lack of a clearly differentiated petiole. The reproductive structures are poorly understood but apparently consisted of "heads" with several platyspermic ovules and numerous elongated scales. These scales have been interpreted as microsporophylls but were probably sterile (Maheshwari & Meyen, 1975). Comparison of these few characters of the Vojnovskyales with the cladogram suggests that the combination of platyspermic ovules (character 9.10) clustered together into heads (character 9.26) could indicate a possible relationship with Bennettitales and *Pentoxylon.* In view of this possibility, a detailed study of the stomata of *Vojnovskya* would be useful, and it would be of considerable interest to compare the scales on *Vojnovskya* "heads" with the interseminal scales of Bennettitales (Harris in Mamay, 1978).

PUTATIVE GNETALES

The Gnetales currently have no well-established macrofossil record (Taylor, 1981a), although this may reflect difficulties of recognition rather than real absence (Arber & Parkin, 1908; Hill & Crane, 1982; Crane & Upchurch, work in progress). Upchurch and Crane (1985) describe a probable gnetalean with attached leaves and seeds from the Lower Cretaceous Potomac Group of Virginia, and pollen resembling that of extant *Ephedra* and *Welwitschia* is widely distributed during the Triassic and early Cretaceous. Recent transmission electron microscope studies of this "gnetalean" pollen have shown that the similarities also extend to the granular exine structure (Trevisan, 1980). Little is known of the plants that produced these grains. The Triassic dispersed pollen *Equisetosporites chinleana* was referred to *Ephedra* by Scott (1960) and has subsequently been demonstrated within microsporangiate cones (*Masculostrobus clathratus* Ash, 1972b; see Zavada, 1984, for details of pollen). The cones consisted of a main axis bearing spirally arranged microsporophylls with microsporangia on the undersurface of an expanded distal lamina. *Bosea indica* is a further microsporangiate structure from the Middle Triassic of Nidpur, India (Srivastava, 1973). It consisted of a stout axis bearing opposite or sub-opposite microsporophylls with unilocular sporangia on the lower surface. The sporangia produced non-saccate, monosulcate pollen with pronounced longitudinal ribs. Neither *M. clathratus* nor *B. indica* is similar to the microsporangiate structures of *Ephedra,* but both could be interpreted as similar to *Pteruchus* in which both dorsiventral and

helical arrangement of microsporophylls occurs (Pant & Basu, 1973). On the basis of cuticular structure Srivastava (1973) suggested that *B. indica* might be part of the plant that produced *Lepidopteris indica* leaves. These similarities with Gnetales and corystosperms require more detailed examination but are of considerable interest in view of the relative positions of these two groups in the cladograms.

A further possible macrofossil record of gnetalean-like plants is *Hexagonocaulon minutum* from the Upper to Middle Triassic of the South Shetland Islands. *Hexagonocaulon minutum* Lacey and Lucas (1981) was established for a large number of small in situ axes, each 0.5–4 mm in diameter. The axes bore alternating whorls of three scale-like bilobed appendages at the nodes. Nothing is known of the reproductive structures, but anatomically they share some similarities with *Equisetites* and *Ephedra* (Lacey & Lucas, 1981).

Another fossil for which a gnetalean relationship has been suggested is the dispersed pollen *Eucommiidites*. *Eucommiidites troedsonii* was described first from the early Jurassic of southern Sweden (Erdtman, 1948) and interpreted as a tricolpate angiosperm grain with unequally developed colpi. Based on analyses of the symmetry, Couper (1956, 1958) suggested that a gymnospermous relationship was more likely, and Hughes (1961) interpreted the grain as distally monosulcate with a proximal zonosulcus. Pollen wall structure of *Eucommiidites* is granular (Doyle et al., 1975), but in some forms there are "pillar-like elements" in the pollen wall (Trevisan, 1980). The gymnospermous affinity of *Eucommiidites* was confirmed by its pollen wall structure (Doyle et al., 1975) and by its occurrence in the micropyles of dispersed seeds from the Lower Cretaceous (Wealden) of southern England (Hughes, 1961), the Lower Cretaceous Patuxent Formation of Virginia (Brenner, 1967), and the Upper Liassic of Poland (Reymanówna, 1968). van Konijnenburg-van Cittert (1971) has described a microsporangiate cone-like structure from the Jurassic of Yorkshire that produced *Eucommiidites* pollen in numerous microsporangia on the adaxial surface of a microsporophyll.

Knowledge of *Eucommiidites* is therefore too fragmentary to permit a detailed evaluation of relationships. However, the granular pollen wall (character 9.21) and the occurrence in ovules with an elongated micropyle suggests the possibility of a relationship with corystosperms, Gnetales, Bennettitales, or *Pentoxylon*. Similar views have been expressed by Hughes (1961), Trevisan (1980), and Doyle et al. (1975). Against this suggestion is the occurrence of a well-developed megaspore membrane in the ovules (Reymanówna, 1968). Further information on the plants producing *Eucommiidites* is clearly required.

LEPTOSTROBUS

Leptostrobus is an ovulate reproductive structure of Jurassic and Lower Cretaceous age. It consists of an axis bearing small scale leaves at the base and widely separated "capsules" containing ovules in the upper region (Harris, 1951a; Harris et al., 1974; Krassilov, 1977b). The "capsules" are sessile and two-valved, with each valve containing a single row of three to eight small ovules. The ovules are poorly known, but were arranged with their micropyles facing the cone axis, and had a resistant megaspore membrane. Based on field association and cuticular similarity, *Leptostrobus* has been attributed to the same plant as *Czekanowskia* and *Solenites*. The leaves are borne on short shoots and may be either simple (*Solenites*) or finely and dichotomously branched (*Czekanowskia*). The microsporangiate organ *Ixostrobus* has been linked with *Czekanowskia* at some localities (Krassilov, 1970), but in the Middle Jurassic flora of Yorkshire the evidence for linking *Leptostrobus cancer* with *Ixostrobus whitbiensis* is weak, and *Ixostrobus* may be attributed equally well to *Desmiophyllum gramineus* (Harris et al., 1974).

Leptostrobus is not well understood, but some inferences concerning its systematic relationships are possible with reference to the cladogram. The presence of scale leaves at the base of the "capsule"-bearing axis suggests that it is morphologically an axial structure. The "capsules" therefore may be homologous to "cupulate" megasporophylls. The valves of the "capsule" could be interpreted either as a single bivalved "cupule" or as a pair of closely associated "cupules" (character 9.19). However, *Leptostrobus* has a resistant megaspore membrane and has several seeds in each cupule (i.e., lacks characters 9.20, 9.22). Its position in the cladogram therefore could be hypothesized as above the level of *Callistophyton* and peltasperms but below that of Gnetales, Bennettitales, and *Pentoxylon*. This hypothesis, however, may conflict with evidence from leaf morphology (character 9.11) and further characters are needed to pursue the issue.

Problems and Possibilities for Future Research

The analysis presented in this paper is open to criticisms of various kinds. However, criticisms of the lack of direct paleobotanical evidence of morphological transitions and the supposed invalidation of the results by pernicious homoplasy are straightforwardly rejected.

The view that "direct" paleontological evidence is the final arbiter in elucidating phylogeny, and therefore in determining phylogenetic relationships, is entrenched in much botanical literature, but the kind of decisive paleontological evidence that might be required or expected is rarely elaborated. Finely graded series of intermediates that can be "read directly from the rocks" are not a common feature of the paleontological record (Crane, 1984), and it is naive to expect the simple description of further fossils to miraculously reveal plant phylogeny. As in other areas of paleontology, paleobotanists will always be faced with a problem of determining phylogenetic relationships between superficially dissimilar organisms without an unequivocal series of intermediates. The problem of determining plant phylogeny is therefore to produce a classification that reflects phylogenetic relationships. To accomplish this effectively requires an explicit method of classification that has a straightforward evolutionary interpretation.

The second common criticism, that homoplasy (parallelism, convergence, and reversal) is so pervasive that the character patterns revealed by phylogenetic analysis are meaningless, is frequently linked to functional arguments that invoke the influence of strong selective pressures. In plants there is certainly considerable homoplasy (Fig. 22). Perhaps this is to be expected in dominantly modular organisms with highly variable genetic mechanisms and the potential for extreme phenotypic plasticity. However, either character patterns are completely meaningless and any attempt to clarify plant phylogeny is abandoned; or the problem becomes how may homoplasy be recognized particularly in cases where the normal criteria of structural, positional, and developmental similarity are fulfilled? Homology may only be differentiated from homoplasy by reference to other characters (Fig. 22). The similar habit of some Euphorbiaceae and Cactaceae is interpreted as convergence because of different relationships that floral characters and other features indicate. The fact that homoplasy can be assessed only in this way leads logically to a search for the simplest nested pattern for explaining the distribution of all features.

More serious, in my view, are problems that involve the analysis of characters on which the cladogram is based. A brief attempt has been made to justify the monophyly of Bennettitales, cycads, conifers, glossopterids, Gnetales, and angiosperms in order to simplify the analysis, but the assumptions involved need to be tested as a more detailed understanding is developed of relationships within these groups. Similarly, generalizations concerning groups of fossil plants such as the medullosans may be shown to be unjustified if future work demonstrates that they are heterogeneous fossil taxa (Beck, 1981: 193). Assumptions about unknown characters in certain fossil plants are also problematic. These were kept to a minimum and are explicitly identified in the character tables. The basis for many is explained in the text, but others were merely scored as plesiomorphic to minimize their influence on patterns of relationships. The necessity for these assumptions highlights the relatively poor understanding of many fossil taxa as whole plants. Current knowledge is highly uneven, and it is clear that there is as much need to understand our present fossils better as to discover new fossil taxa (Harris et al., 1974: 85).

Recognition of these problems has highlighted specific questions that need to be addressed by future neontological and paleobotanical research. Those particularly important to resolving the relationships between "Mesozoic seed ferns," Bennettitales, Gnetales, and angiosperms are:

a) Clarification of integument ontogeny, anatomy, and vasculature in peltasperms, *Caytonia,* corystosperms, and particularly in glossopterids.

b) Clarification of the manner in which microsporophylls and megasporophylls were borne in peltasperms, glossopterids, *Caytonia,* and corystosperms. Reexamination of the corystosperms would be particularly useful to reveal details of megasporophyll construction and the morphology of ovules and cupules. Further study of silicified glossopterid material should also clarify the relationship between the megasporophyll and "subtending bract."

c) Comparison of the outer seed covering ("cupule") of *Vardekloeftia* with the outer integumentary layer of anatomically preserved Bennettitales and *Pentoxylon.*

d) Comparison of the anatomy and biology of bennettitalean, gnetalean, and angiosperm ovules,

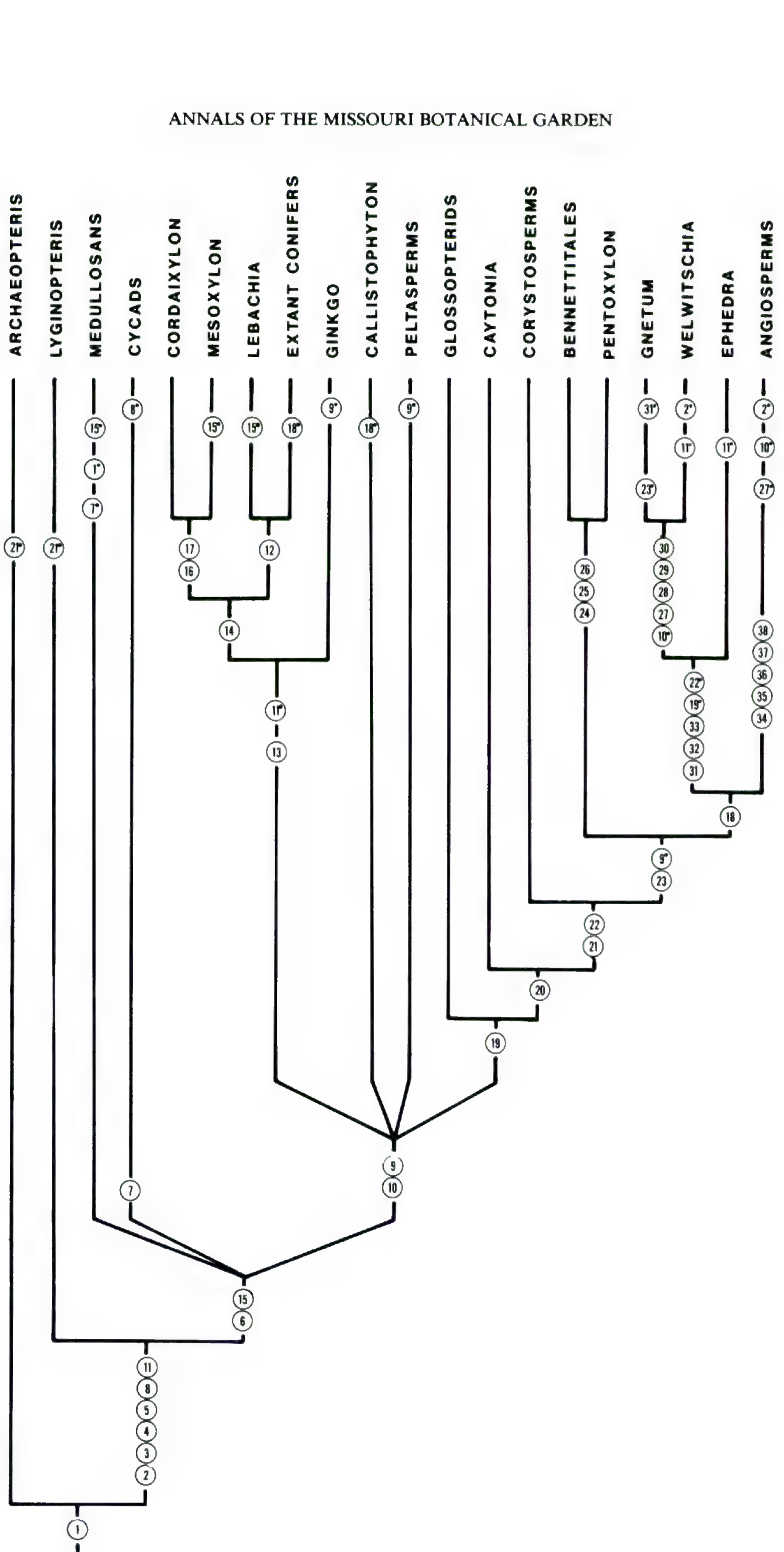


FIGURE 22. Relationships between major groups of seed plants. Strict consensus tree derived from ten equally parsimonious cladograms constructed from version two of the data matrix. In this analysis the "cupules" of

and detailed evaluation of the evidence for platyspermy in these taxa, especially angiosperms.

e) Comparative study of "seed cuticles," including the megaspore membrane in living and fossil plants using modern techniques (Hill & Crane, 1982).

f) Comparative study of pollen wall stratification in "Mesozoic seed ferns," *Pentoxylon,* and Bennettitales.

g) Attempts to identify the plants producing dispersed Mesozoic "*Ephedra*-like" pollen.

Further difficulties with the analysis are the use of "reduction" or "loss" characters, e.g., lack of archegonia (character 9.29) and the relatively small number of characters available. It is a tenuous position to regard two taxa as identical with respect to a condition that cannot actually be observed, but such characters may provide useful synapomorphies if they can be correlated with other features.

Similarly, examination of additional features clearly is desirable but is constrained in part by lack of comparative information for seed plants as a whole, including living representatives. In many cases characters that have been surveyed in detail in one group of seed plants have been examined only cursorily, or not at all, in others. Most botanical comparative studies have concentrated on taxa within seed plants and, as a result, have tended to reinforce their apparent differences.

Conclusions

The approach outlined in this paper does not differ fundamentally from approaches previously used in paleobotany to interpret early land plant evolution (Banks, 1975; Chaloner, 1970b), early angiosperm evolution (Doyle, 1978; Doyle & Hickey, 1976), and studies of the major patterns of angiosperm leaf architecture (Hickey & Wolfe, 1975). It differs only in being relatively explicit and in attempting to define a highly resolved hierarchy of relationships. In the context of seed plants it has attempted, for the first time, to provide a detailed scheme of relationships accounting for both neontological and paleontological data.

The characters considered support a monophyletic origin of seed plants. *Lyginopteris* is placed as the sister taxon to all other seed plants. Flattened seeds and saccate pollen together define a major group of seed plants ("platysperms") including conifers, cordaites, *Ginkgo, Callistophyton,* peltasperms, glossopterids, *Caytonia,* and corystosperms. If the outer integument of bennettitalean, *Pentoxylon,* and angiosperm bitegmic ovules is homologous to the "cupule" of glossopterids, *Caytonia,* and corystosperms then these groups plus the Gnetales form a clade of "higher" "platysperms" within the "platysperm" group. Such an interpretation would reconcile the widely accepted view that "Mesozoic seed ferns" are highly relevant to the problem of angiosperm origins with the idea proposed at the beginning of this century that Bennettitales and Gnetales are closely related to flowering plants. If this is accepted the corystosperms are the sister group to the "higher platysperms." The Bennettitales and *Pentoxylon* are resolved as sister taxa and together form the sister group of angiosperms plus the Gnetales. The Gnetales are monophyletic and the sister group of flowering plants.

This pattern of relationships precludes any close phylogenetic connection between cycads and Bennettitales and emphasizes the heterogeneity of the seed ferns as currently recognized. The seed ferns include taxa of very diverse relationships. The current concept of the pteridosperms is therefore phylogenetically meaningless and confuses discussions of phylogenetic relationships.

The interpretation of seed plant relationships presented in this paper (particularly cladogram 2) is in broad agreement with the first stratigraphic appearance of the various taxa. It suggests that increased understanding of Triassic Bennettitales, Gnetales, and corystosperms will be of major interest in further elucidating the phylogenetic relationships of flowering plants. It may also suggest a substantially earlier time of origin for the flowering plant clade than is currently envisaged.

A Triassic or Jurassic origin would not conflict with the hypotheses of angiosperm diversifica-

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Bennettitales and *Pentoxylon* were coded as homologous to the "cupules" of glossopterids, *Caytonia,* corystosperms, and angiosperms. Bennettitales and *Pentoxylon* were coded as apomorphic for characters 9.19, 9.22, and 9.25. Total characters 38, character state transitions 62. A dot next to the number indicates homoplasy.

tion proposed by Doyle and Hickey (1976) and would suggest a pattern of evolutionary history for flowering plants similar to that of mammals with an early Mesozoic origin followed by low diversity and a delayed radiation. There are still, however, no unequivocal pre-Cretaceous angiosperm records, although there is an abundance of enigmatic Mesozoic plants about which we know almost nothing. Among these problematica that show angiosperm-like characters are the following: *Furcula* (Harris, 1932a), *Marcouia* (Ash, 1972a), *Scoresbya* (Kräusel & Schaarschmidt, 1968), and *Phyllites* (Seward, 1904). In palynology, the reticulate, columellate, monosulcate grains reported by Cornet from the Upper Triassic–Lower Jurassic Newark Supergroup of the eastern United States are very similar to those of angiosperms (Doyle, 1978).

The principal difficulty with the phylogenetic analysis presented in this paper is the problem of dealing with missing characters in many potentially critical fossil plants. However, recognition of important areas of ignorance is of value in providing a focus for future paleobotanical work with phylogenetic objectives. The tests of the hypotheses presented here will come from future paleobotanical discoveries and the careful application of additional characters from neobotanical and paleobotanical research.

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BIOLOGICAL DIVERSIFICATION AND ITS CAUSES[1]

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ABSTRACT

Three major patterns of diversity are defined and a general hypothesis proposed to explain them. These patterns include (a) macroevolutionary diversity, encompassing temporal changes in species richness within and among clades, (b) global diversity, in which gradients of diversity among communities or biotas vary spatially and temporally, and (c) Phanerozoic diversity, which describes large-scale temporal variation in species richness within the entire biosphere. Current explanatory hypotheses for these patterns are generally formulated for systems that are assumed to be in a state of ecological equilibrium, with speciation and extinction rates being diversity-dependent. This paper describes an alternative model of diversification in which speciation and extinction rates are independent of standing diversity.

It is postulated that speciation rate is controlled primarily by large-scale changes in lithospheric (geomorphological) complexity. This hypothesis is a deductive consequence of biological data showing that allopatric speciation is the general mode of differentiation, and of geological data showing that tectonic changes within the lithosphere are responsible for the formation of geographic and ecological barriers. This hypothesis makes a number of predictions about patterns of endemism, historical biogeography, and spatial gradients of diversity, and data consistent with these predictions are presented. Other potential regulators of speciation rate (degree of morphogenetic variability within species, behavioral-ecological variability within species, intensity of sexual selection) are discussed and their potential roles in shaping diversity patterns are evaluated. Although they may occasionally be important for explaining some intracladal patterns of diversification, they are insufficient by themselves to account for spatial patterns or long-term changes of diversity within biotas.

Extinction rate is postulated to be controlled primarily by spatial and temporal changes in environmental harshness, particularly as the latter is manifested by gradients of temperature and moisture. Considerable neontological and paleontological data suggest that change in harshness is a major factor shaping temporal and spatial patterns of diversity through its effects on extinction rate. Other causal mechanisms of extinction, particularly the tectonic elimination of habitats, may be of importance for specific groups of organisms (e.g., marine shelf communities following continent–continent collisions) at specific localities and times (e.g., near a volcanic eruption) but are not likely to play as important a role as does change in harshness.

Together, the two main controls on speciation and extinction define a diversity-independent process of diversification. The biosphere can be viewed as an open thermodynamic system that can be expected to grow in complexity (including diversity) through time as a result of the inflow of matter and energy. This increase in complexity is constrained by external factors (physical changes in the biosphere or atmosphere such as ice ages) rather than by processes intrinsic to the biosphere itself (e.g., species interactions). The temporal history of the biosphere therefore has been nonequilibrial rather than equilibrial.

Clades of organisms exhibit variation in diversity through space and time, and closely related clades often are characterized by significant differences in relative diversity. Species diversity in large-scale community assemblages (biotas) varies geographically, and the relative abundances of species are apportioned nonrandomly within and among local habitats. These and other patterns of biotic diversification have been known for a long time and biologists have fervently sought their explanation. This paper addresses this question: Can a major component of the observed variance in these patterns be explained by a single causal hypothesis?

The analysis of biological diversification has recently shifted its emphasis. For many years, particularly in the 1960s, the field was dominated by the study of large-scale and local patterns of

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species diversity, particularly from an ecological point of view. Since the early 1970s, the problem of diversification has been addressed increasingly from a taxonomic viewpoint, especially by paleontologists. This change has arisen partly as a result of a reformulation of macroevolutionary analysis, from one focusing on the adaptive transformation of organismal form to an analytical assessment of changes in diversity within and among clades (Eldredge & Gould, 1972; Stanley, 1979; Eldredge & Cracraft, 1980; and many papers in *Paleobiology*). As a consequence, the literature is now dominated by the study of speciation and extinction rates using primarily fossil taxa. Significantly, while attempting to account for patterns of diversification within clades and for temporal changes in the entire biosphere, this work has often neglected the spatial analysis of diversity.

Many explanations have been proposed for patterns of diversification, yet there has been little recognition that macroevolutionary diversity and spatial diversity might constitute a single problem. Biologists realize that complex biological patterns such as those of diversity only rarely result from single causal processes. Yet, science is an endeavor that searches for generality, and thus scientific explanations, to the extent that they are in fact general, should attempt to account for as much of the variance within a dataset as possible. In so doing, patterns not explained by that hypothesis may be identified and perhaps explained by second order causal factors.

Patterns of diversification are first-order functions of speciation and extinction. A theory of biological diversification, therefore, must begin by delineating the rate-controls of speciation and extinction. This paper advances the hypothesis that spatiotemporal changes in speciation and extinction rates describe patterns of diversification both within clades and across large-scale species assemblages. In particular, diversification is postulated to be diversity-independent, with speciation rate being a function of the rate-change in lithospheric (geomorphological) complexity and extinction rate being a function of the rate-change in environmental harshness. This hypothesis makes the claim of identifying the major causal factors shaping these diversity patterns. Other factors certainly will be of importance in particular instances, and some of these will also be discussed below. Intra- and intercladal changes in species abundances and large-scale spatial gradients in diversity constitute the domain of the hypothesis, and it makes no attempt to account for local, among- or within-habitat diversity. Contemporary diversification theory is based largely on the assumption that the controls of speciation and extinction are diversity-dependent. The theoretical basis of diversity-dependent models has been evaluated elsewhere (Cracraft, in prep.) and will not be considered in detail here.

Biotic Diversification

THE PATTERNS

Patterns of diversity (species richness) can be expressed in terms of the diversifying lineages (clades) themselves, in which case these can be called macroevolutionary patterns (Eldredge & Cracraft, 1980; Cracraft, 1982a), or they can be characterized spatially as a statistical summation of all the cladal patterns present at one or more locations. These latter patterns of diversity will be termed global when the scale is large, and local (or ecological) when it is small.

Brief mention should be made of several assumptions underlying the recognition of diversity patterns (discussed in detail in Cracraft, 1981a, 1982a). In defining diversity, we seek to count all those taxonomic entities thought to be evolutionary units. Thus, concepts of species have important theoretical and empirical consequences. To the extent that prevailing species concepts vary from group to group, measures of diversity will not necessarily be comparable. Within much of vertebrate zoology (especially in ornithology and mammalogy), the biological species concept is widely applied (e.g., Mayr, 1963, 1969). That this species concept cannot be used to describe diversity accurately is not generally understood. Many differentiated, evolutionary taxonomic units, for example, can be included within a single "biological species," and this often occurs in practice (Rosen, 1978; Cracraft, 1983a). Use of the biological species concept significantly underestimates the numbers of taxa that have diversified. It is more appropriate, therefore, to adopt a species concept that is defined in terms of the evolutionary units themselves and thus accurately describes their relative abundances, both phylogenetically within clades and ecologically within and among biotas (for one such concept, see Nelson & Platnick, 1981, and Cracraft, 1983a).

Patterns of diversity can be described accurately only to the extent that highly corroborated

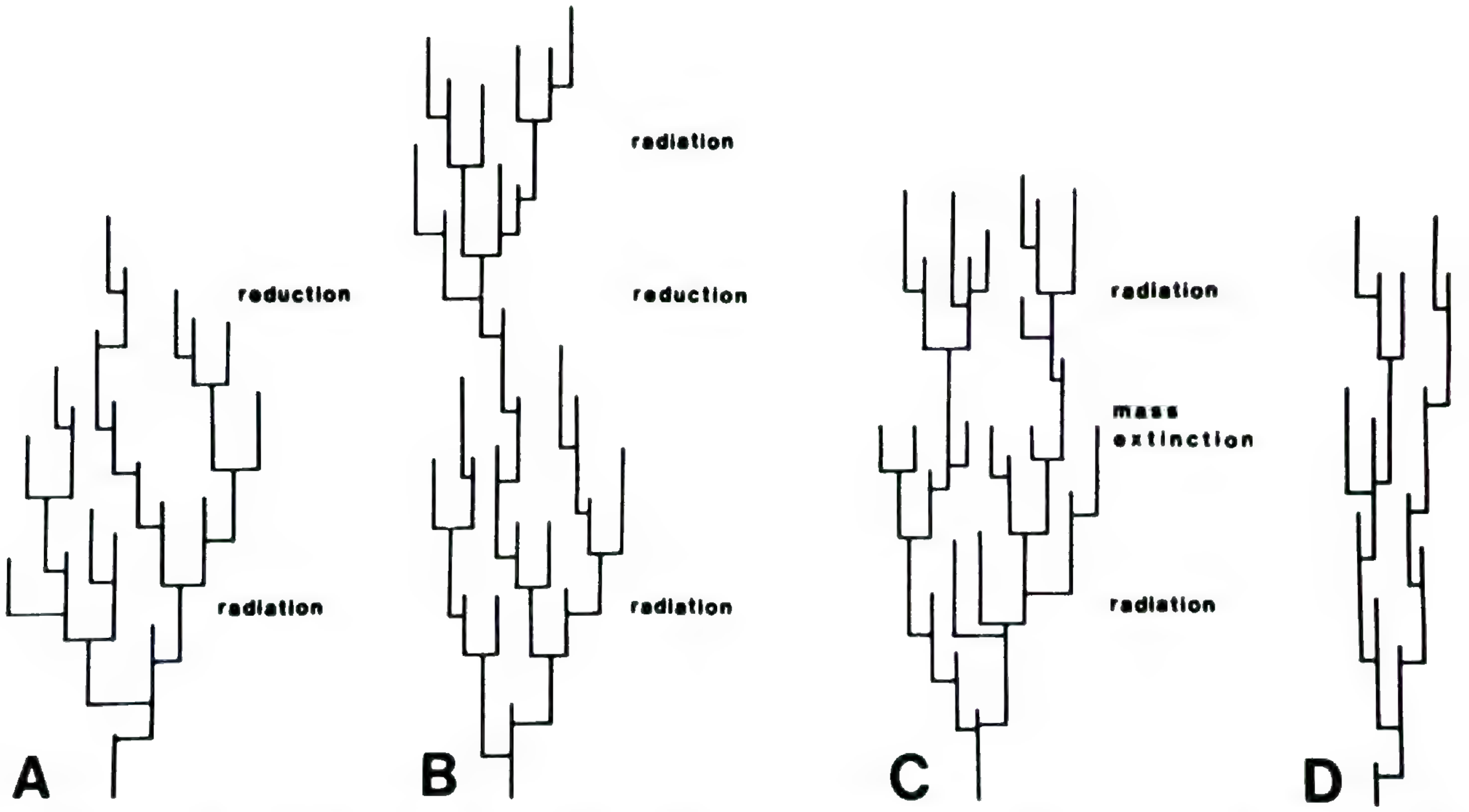

FIGURE 1. Four common patterns of diversity observed within lineages. Patterns A–C involve combinations of radiation and reduction diversity; pattern D illustrates steady-state diversity (after Cracraft, 1982a).

phylogenetic relationships are available. This is especially true with respect to macroevolutionary patterns, which are defined in terms of those relationships. Different hypotheses of relationships can change patterns of diversity significantly (Cracraft, 1981a, 1982a; Novacek & Norell, 1982). Knowledge about phylogenetic relationships may be less critical when diversity of biotas is being measured, unless that measure is being partitioned taxonomically or examined historically.

Three major kinds of diversity patterns will be addressed in this paper:

1. *Macroevolutionary diversity.* This includes patterns of species richness within and among clades. Intra-cladal patterns are expressed in terms of *radiation diversity,* in which species numbers increase with time; *reduction diversity,* in which numbers decrease with time; and *steady-state,* in which diversity is maintained relatively constant throughout time. These patterns may occur in combination within any one clade (Fig. 1).

A second macroevolutionary pattern describes sister-clades that vary greatly in relative diversity (Table 1). Because they are hypothesized to be sister-groups, the diversity of the two clades can be compared in terms of the same age of origin.

2. *Global diversity.* Large-scale gradients of species richness among communities constitute a well-known pattern, particularly as it is expressed in terms of latitude, but longitudinal gradients also exist. Many such patterns have been described in the literature (e.g., Fischer, 1960; Stehli, 1968), and some will be discussed below.

3. *Phanerozoic diversity.* Temporal variation in species richness within the biosphere has been extensively studied, particularly for marine organisms (Raup, 1972, 1976a, 1976b; Sepkoski, 1976, 1978, 1979).

EQUILIBRIUM OR NONEQUILIBRIUM?

Current models of diversification generally have borrowed their conceptual framework from population ecology. Speciation rate is analogized with birth rate, extinction rate with death rate. Then, assuming an upper limit to diversity, speciation and extinction rates are taken to be diversity-dependent, with species richness attaining an equilibrial value. The impetus for this approach, even in those studies examining patterns over vast stretches of time, appears to have been the widespread acceptance of island biogeographic theory (MacArthur & Wilson, 1963, 1967). The use of diversity-dependent, equilibrial models is pervasive, and they have been applied whether the system under discussion is diversity within the entire biosphere through the Phanerozoic (Stehli et al., 1969; Sepkoski, 1976,

TABLE 1. Some avian and mammalian sister-taxa showing significant differences in diversity probably related to tachytelic and bradytelic rates of speciation.

	Tachytelic Taxon	Bradytelic Taxon
Aves[a]	Pelecaniformes	
	other pelecaniforms (59)	Phaethontidae (3)
	Ciconiiformes	
	Ardeiidae (62)	Balaenicipitidae (1)
	Anseriformes	
	Anatidae (147)	Anhimidae (3)
	Falconiformes	
	Accipitridae + Falconidae (279)	Pandionidae (1)
	Galliformes	
	Cracidae + Phasianidae (256)	Megapodiidae (12)
	Gruiformes	
	Rallidae (142)	Heliornithidae (3)
	Columbiformes	
	Columbidae (306)	Pteroclididae (16)
	Cuculiformes	
	Cuculidae (129)	Musophagidae (18)
	Strigiformes	
	Strigidae (135)	Tytonidae (11)
	Piciformes	
	Picidae (204)	Indicatoridae (16)
	Passeriformes	
	other suboscines (1,097)	Acanthisittidae (4)
	Furnariidae (218)	Dendrocolaptidae (52)
	Laniidae (74)	Vangidae (13)
	Corvidae (106)	Grallinidae (4)
	Estrildidae (136)	Bubalornithidae (2)
	Estrildini (113)	Viduini (10)
Mammalia[b]	Chiroptera (981)	Dermoptera (2)
	Rodentia (1,728)	Lagomorpha (66)
	Rodentia + Lagomorpha (1,794)	Macroscelidea (21)

[a] For a discussion of these interrelationships see Cracraft (1981b).
[b] For a discussion of these interrelationships see Novacek (1982).

1978, 1979, 1984; Raup, 1976a, 1976b; Raup et al., 1973; Simberloff, 1974; Webb, 1976; Gould, 1976; Stanley, 1979; Valentine, 1980; Carr & Kitchell, 1980) or diversity within Recent communities (Hutchinson, 1959; MacArthur, 1965, 1972; MacArthur & Wilson, 1963, 1967; Wilson, 1969; Terborgh, 1973; Saunders & Bazin, 1975; Rosenzweig, 1975; Levinton, 1979; Fowler & MacMahon, 1982).

The use of diversity-dependent, equilibrial models has influenced our understanding of diversification in two ways:

1. *By an expectation of pattern.* Observations are theory-laden and our expectation of patterns in nature is dependent on the predictions of our theoretical worldview. By building an equilibrial viewpoint into diversification models, however, expected and observed patterns are more likely than not to confirm (and conform to) that viewpoint. Thus, many paleontologists have interpreted the Phanerozoic diversity curve to be equilibrial (e.g., Sepkoski, 1978, 1979; see Discussion), with mass extinctions perturbing diversity away from the equilibrium, but only for relatively short periods of time. Likewise, the expectation of pattern is also prevalent when diversity-dependent models are applied to patterns of species diversity at the local level. Some of these latter observational expectations include: saturation of habitats, competitively structured community assemblages, predominance of density-dependent mortality, and the presence of limiting similarities among co-existing species, to name only a few (see Wiens, 1984, for further examples and discussion).

Perhaps the major expectation (or assumption) of diversity-dependent models is that there is an upper limit to diversity (MacArthur, 1969; Margalef, 1972; Van Valen, 1976; Levinton, 1979). The upper-limit hypothesis has its strongest rationale within current ecological theory when attempts are made to explain within-habitat diversity, but it also has been extrapolated to the biosphere as a whole. I will return to this hypothesis in the Discussion.

2. *By an expectation of process.* Underlying assumptions also carry with them explicit expectations about the causal structure of nature. As noted, acceptance of an equilibrial worldview has resulted in the widespread use of diversity-dependent models of speciation and extinction rate-control. Metaphorically speaking, the biosphere is viewed as a large *Tribolium* population bottle, in which space and resources are assumed to be limited; then, using the same logistic growth equations of population biology, paleontologists have extended the analogy to expect a decrease in speciation rate and rise in extinction rate with increasing diversity (MacArthur, 1969; Valentine, 1973; Rosenzweig, 1975; Sepkoski, 1978; Carr & Kitchell, 1980). Diversity-dependent "control" of these rates is postulated to result directly from intensified ecological interactions as diversity increases, in particular increased competition and species packing, along with reduced dispersal ability (see above cited authors for a more detailed explanation and Cracraft, in prep. for a critical evaluation of this model).

The hypothesis presented here states that the patterns and processes of biological diversification are more properly characterized within a diversity-independent, nonequilibrial framework. There are several reasons for applying this conceptual approach to questions within evolutionary biology. One is that historical systems, whether physical or biological, behave as if they are nonequilibrial rather than equilibrial, and therefore it seems appropriate that their description be cast in nonequilibrial terms (Mercer, 1981; Peacocke, 1983). Biological systems, including individual organisms, species, communities, and the biosphere, appear to exhibit a transformational history of increasingly more organized steady-states; with rare exceptions, they increase in complexity through time. Thus, an increasing number of biologists have applied nonequilibrial ideas to questions about the origin of macromolecular complexity (Prigogine et al., 1972; Saunders & Ho, 1976, 1981; Wicken, 1978, 1979, 1980; Eigen, 1971; Eigen & Schuster, 1977, 1978a, 1978b), general evolutionary theory (Wiley & Brooks, 1982; Brooks & Wiley, 1984), developmental biology (Zotin, 1972; Lurie & Wagensberg, 1979), and community structure and evolution (Gallaucci, 1973; Ulanowicz, 1980; Phipps, 1981; Johnson, 1981).

A second reason for considering a nonequilibrial approach is that it creates an alternative way of conceptualizing or modeling evolution. Nonequilibrial systems are inherently transformational and nongradualistic when seen macroscopically (Mercer, 1981; Wiley & Brooks, 1982). In contrast, equilibrial systems, by their nature, are not persistently transformational, and within this conceptual framework biologists frequently have constructed elaborate hypotheses to explain the "forces" maintaining the system at or near equilibrium, or returning that system to equilibrium following a perturbation by some outside "force." A nonequilibrial viewpoint places the description of biological systems behavior in a new light.

THE DIVERSITY-INDEPENDENT RATE-CONTROL OF SPECIATION

The primary aim of this section is to describe a hypothesis of speciation rate-control that is diversity-independent. Other factors have also been hypothesized to modulate the rate of speciation, and these will be discussed separately.

THE HYPOTHESIS OF LITHOSPHERIC COMPLEXITY

That speciation rate is controlled primarily by nonequilibrial changes in large-scale lithospheric (geomorphological) complexity can be deduced from biological and geological premises. The hypothesis itself can then be used to generate testable predictions about patterns of biological diversification. Consider two biological and two geological premises:

Premise 1. Speciation is a geographical phenomenon and is allopatric in most groups of organisms (Mayr, 1963; Grant, 1971; Bush, 1975; White, 1978).

Speciation via genetic alterations such as polyploidy is frequent in some groups, particularly angiosperms (Grant, 1971; White, 1978), but there is little evidence to suggest that allopatric differentiation is also not prevalent in these taxa. In both plants and animals, sister-species are usually observed to be allopatric. For example, within tephritid flies of the genus *Rhagoletis,*

which has been studied extensively because it is said to provide a possible example of sympatric speciation, most of the species are allopatric and almost certainly exhibited geographic disjunction during their diversification [Bush (1966); see also the arguments of Futuyma & Mayer (1980) against the commonness of non-allopatric differentiation].

Premise 2. Allopatric speciation is dependent upon the origin and maintenance of geographic or ecological barriers.

This assumption is straight-forward and empirically well-corroborated (Mayr, 1963; Bush, 1975; White, 1978). Geographic barriers are important in two ways, by promoting vicariance and isolation of widespread populations and by providing the possibility of isolation given long-distance dispersal across those barriers. Although not dependent upon an assumption about the relative frequencies of vicariance and long-distance dispersal, the hypothesis can be used to predict spatial characteristics of differentiation (see below).

Premise 3. The lithosphere is an irreversible thermodynamic system exhibiting a nonequilibrial increase in complexity.

Decay of radioactive isotopes of uranium, thorium, and potassium produces heat that ultimately drives mantle convection currents and lithospheric plate motion (Davies & Runcorn, 1980; Bott, 1982). Being a historical system, the lithosphere is irreversibly transformational. Geological degradation of complexity may occur locally (for example, from erosional processes), but the overall historical trend has been for complexity to increase globally, as evidenced by our ability to reconstruct past lithospheric (geomorphological) configurations.

Premise 4. The rate of formation of geographic and climatic barriers is a function of rate-changes in lithospheric (geomorphological) evolution.

Relative plate motions create large-scale geomorphological complexity in some areas and contribute to processes of geological degradation in others. Regions of high complexity (e.g., areas of high relief) are generally associated with highly active, converging plate margins or with active deformation within plates. Changes in the lithosphere also have first-order effects on climatic change (Hamilton, 1968; Cox, 1968; Crowell & Frakes, 1970; Frakes & Kemp, 1972, 1973) and thus on the rate of climatic barrier formation.

These premises lead to the hypothesis that *the rate of speciation is a first-order function of lithospheric (geomorphological) complexity.* A causal connection between speciation and large-scale plate motions has been suggested before (see especially Valentine & Moores, 1970, 1972; Valentine, 1971, 1973; Bakker, 1977). Simpson (1964) and Nel (1975) also noted a correlation between geologic (topographic) complexity and diversity, thereby inferring a relationship to speciation. Bakker (1977) postulated cycles of orogeny and marine transgressions producing cycles of speciation in the highlands of continents, with subsequent immigration (dispersal) of species into lowland habitats. Ross (1972), in a highly stimulating and underappreciated paper, viewed diversification as a rate-function of geographic disjunction within a nonequilibrium biosphere; his short contribution is one of the more explicit statements to date regarding the rate-control of speciation by earth history.

The hypothesis of lithospheric complexity described here differs significantly from this previous work. It states explicitly that the rate-change of geological complexity is the primary control of speciation rate. The hypothesis also makes a larger claim: because the lithosphere exhibits a nonequilibrial increase in complexity through time, Phanerozoic patterns of diversification should also be nonequilibrial. Furthermore, the hypothesis is more general: although it acknowledges the correlation between high topographic relief and high diversity, it posits a causal relationship between lithospheric complexity and speciation rate across both terrestrial and marine environments. Thus, topographic relief per se is not the central causal agent of speciation control; rather, it is the rate-change in geomorphological complexity that is causally related to the rate at which barriers arise and taxa therefore speciate. Areas of high relief may be geologically stable and produce few species, whereas areas of lower relief may be tectonically active and produce species at a higher rate.

We now turn to some predictions and implications of the hypothesis of lithospheric complexity and examine observational data relevant to them. Critical problems exist with any attempt to decipher the causal mechanics of diversification. If we are examining the expected influence of a particular causal hypothesis (as with lithospheric complexity, for example), not only are there the confounding contributions of other factors controlling the rate of speciation, but also

the concomitant effects of extinction. Except under very special circumstances, we cannot expect to measure speciation rates directly and accurately. Consequently, diversity patterns themselves constitute the data with which we must test alternative causal processes. However, diversity patterns are the end result of the spatiotemporal history of all the separate causes of speciation *and* extinction. Therefore, predictions derived from any one hypothesis of speciation or extinction rate-control must of necessity be proposed within the context of *ceteris paribus.* This requirement naturally raises the specter of ad hoc escapes from potentially conflicting observational data: if the data do not fit the hypothesis being tested, are we to claim that the hypothesis itself is not rejected because deviations from expectation can be ascribed to other causal factors? This onerous problem can rarely be avoided when many causal factors are involved; one can only attempt to discuss its ramifications as openly as possible (e.g., see Hillborn & Stearns, 1982). This situation does *not* mean that causal hypotheses about speciation and extinction rate-controls are untestable; as long as the relative influence of other potential causal factors can be minimized, then the importance of a specific causal mechanism can be investigated.

A series of predictions can be derived from the hypothesis that geomorphological change controls the rate of speciation, including:

Prediction 1. Species will be distributed nonrandomly and will be clustered in areas of endemism.

If geomorphological change mediates the spatial pattern and tempo of speciation, then geologically induced barriers (physiographic or ecological-climatic) will partition biotas through time, and thus produce common areas of endemism. This is a strong prediction, but the expected patterns can be obscured (1) by population dispersion in which case species ranges will exhibit varying degrees of congruence, or (2) by long-distance dispersal across barriers. If taxonomic differentiation took place *only* by long-distance dispersal and not by the vicariance of species that were already widespread, then the frequency of well-defined areas of endemism would be low. Long-distance dispersal is a stochastic property of individuals, and thus major centers of endemism are not likely to arise by this process. In summary, if areas of endemism did not exist, or were very uncommon, then the hypothesis of lithospheric complexity would not be corroborated.

Observational data strongly support this prediction. It has been known for several centuries that organisms are nonrandomly distributed and cluster in areas of endemism. The literature pertaining to areas of endemism (also termed "areas of provinciality," or "centers of dispersal") is vast. For example, well-marked areas of endemism are apparent in the avifaunas of Australia (Keast, 1961); Africa (Hall & Moreau, 1970; Snow, 1978), and South America (Muller, 1973; Haffer, 1978; Cracraft, 1985). Likewise, Gentry (1982a) and Prance (1982a, 1982b) have presented data documenting the existence of areas of endemism within the South American flora. Many more examples could be cited.

Prediction 2. Species will exhibit congruent patterns of historical biogeography.

There is no stronger test of the hypothesis of lithospheric complexity than the relative frequency of congruent biogeographic histories of clades whose species are endemic in the same areas (Rosen, 1978, 1979; Platnick & Nelson, 1978; Nelson & Platnick, 1981; Cracraft, 1982b, 1983b). The vicariance of biotas is the only known mechanism producing congruent histories involving three or more areas of endemism; the other mechanism producing allopatric disjunction, long-distance dispersal, can yield two-area congruence (as from a mainland to an island), but invoking it to explain patterns involving three or more areas necessitates accepting countless ad hoc assumptions about dispersal, the relative timing of differentiation, and extinction (see above citations).

Thus, the degree to which phylogenetic relationships of species confirm the existence of congruent biogeographic patterns is a direct estimate of the rate-control of speciation by geologic (including climatic) fragmentation. Unfortunately, the field of vicariance biogeography is still in its infancy, and few studies bearing on this prediction have been completed. Nevertheless, several investigations corroborate the hypothesis in that they have discovered congruent patterns. Rosen (1978, 1979) documents an example using Central American freshwater fishes; Cracraft (1982b, 1983a, 1983b) does likewise for some Australian birds; Wiley and Mayden (1985) also present strong evidence that vicariance was extremely important in the diversification of the eastern North American fish fauna. Finally, the Amazonian forest avifauna also presents examples of

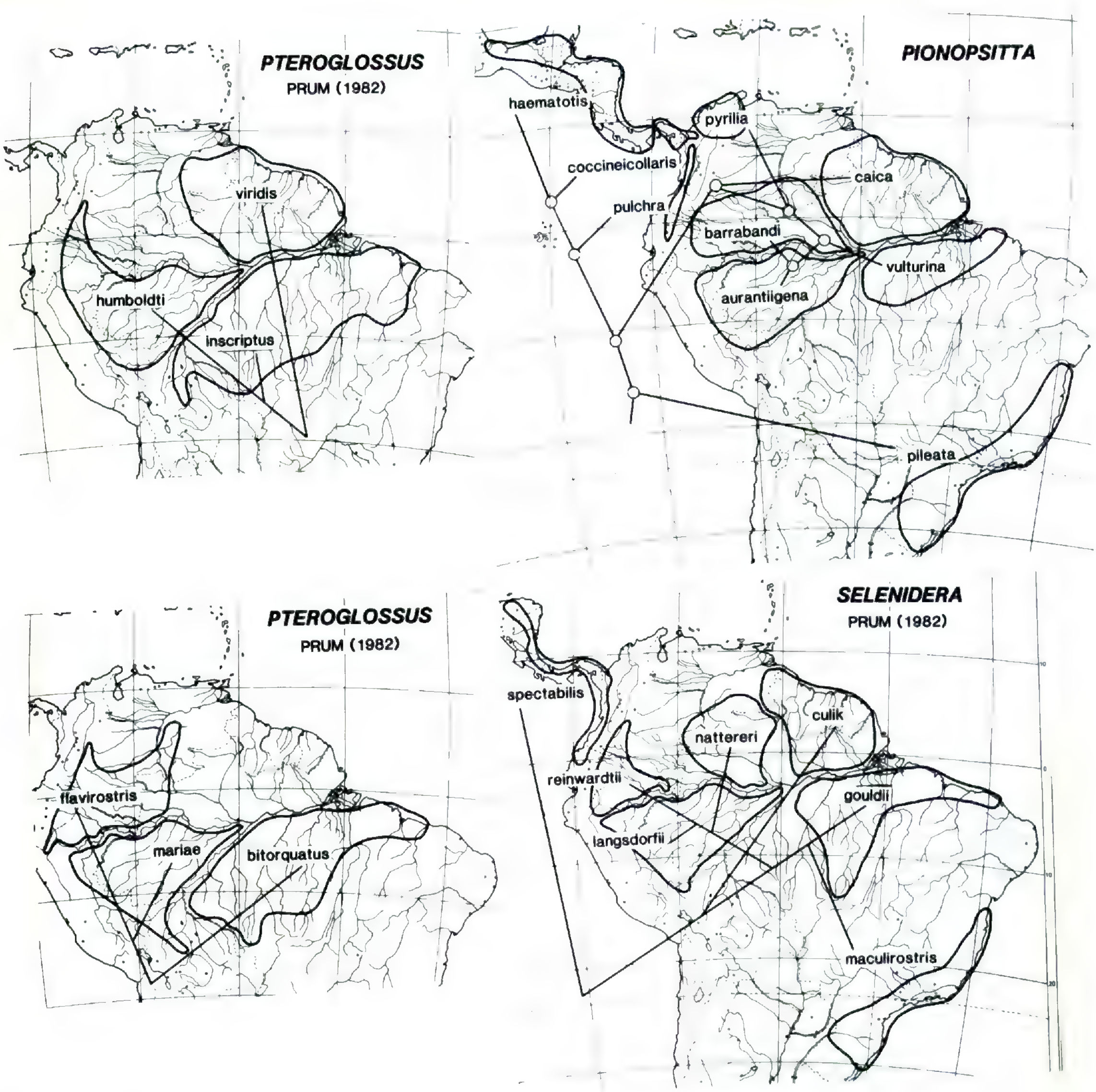

FIGURE 2. Four lineages of tropical South American birds exhibiting congruence for four areas of endemism in Amazonia. The phylogenetic patterns within these clades indicate the following pattern of historical biogeography: northeast Amazonia + [southeast Amazonia + (northwest Amazonia + southwest Amazonia)]. This congruence implies that the biota within this area was segregated via geological or ecological vicariance events (see text). Other taxa in Central America, northwest South America, and southeast Brazil represent unique components in these comparisons. Data after Prum (1982) and Cracraft (unpubl. observ.).

taxa whose biogeographic patterns are congruent with one another (Prum, 1982; Cracraft, unpubl. observ.; see Fig. 2).

Congruent biogeographic histories such as these are compelling support for the hypothesis of lithospheric complexity. That congruence implies that the biotas themselves have been fragmented by common geographic barriers, and if so, we can predict that other taxa endemic in these same areas eventually will be shown to have histories congruent with those already studied. If geological change has not set the tempo of diversification, or has played only a minor role, then biogeographic congruence should be rare or nonexistent.

Prediction 3. Geographic gradients in species diversity will parallel gradients in lithospheric complexity.

All things being equal, species diversity should be higher in regions of higher complexity. But things are rarely, if ever, equal. Regions of lower complexity might have higher diversity if extinction has been significant in those regions of higher complexity. Thus, in attempting to ex-

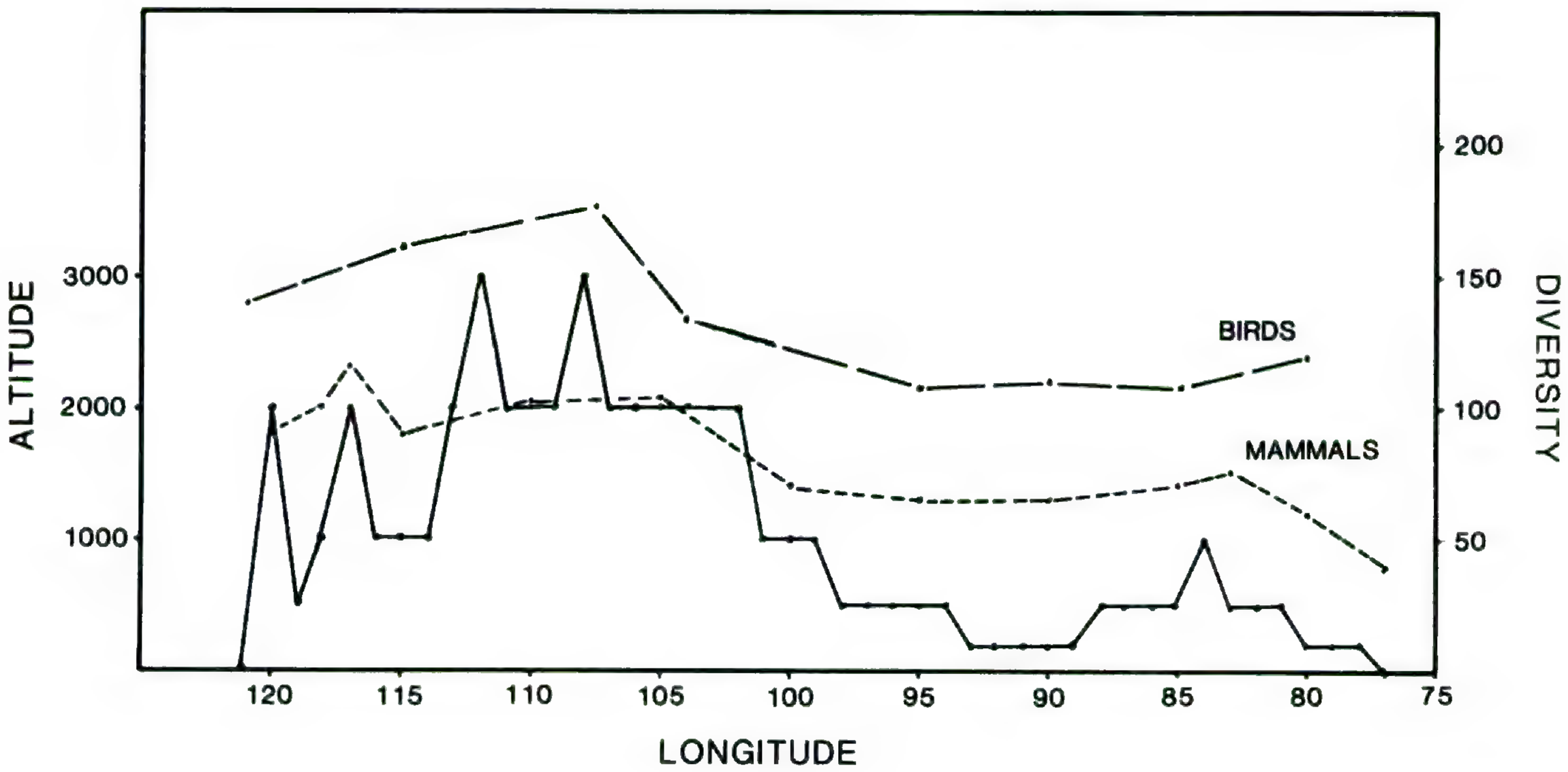

FIGURE 3. A longitudinal transect across the southern United States at 35°N latitude showing the relationship between topographic (geomorphological) complexity and species diversity gradients of birds and mammals (data from MacArthur, 1969; Simpson, 1964). Diversity in both groups rises in those areas having the greatest topographic complexity (see text).

amine this prediction, it is important to minimize the potential effects of variation in extinction along the geographic transect being investigated. As will be discussed below, this is probably one of the reasons why latitudinal transects of diversity do not show close correlation with complexity. Longitudinal transects, on the other hand, can be chosen so as to reveal the relationship between diversity and complexity while at the same time minimizing the influence of extinction in obscuring that pattern.

Consider first data from a continental setting. Figure 3 shows a longitudinal transect across the southern United States at 35°N. In this figure, relative topographic relief is taken to be an approximation of lithospheric (geomorphological) complexity. Data on species richness for mammals (Simpson, 1964; Wilson, 1974) and land birds (MacArthur, 1969; see also Cook, 1969) are also displayed. The gradient in diversity of both birds and mammals parallels the gradient in topographic complexity, as predicted by the hypothesis. [Simpson (1964: 70) noted as a "speculative possibility" the idea that high topographic relief might have promoted more speciation in the West (see also Cook, 1969).]

Comparable data for similarly chosen gradients are rare indeed, in part because the taxa being analyzed must not be sensitive to any marked change in environmental harshness along the gradient. Thus, it is not surprising that amphibians exhibit a strong westward decrease in diversity along the same transect (Kiester, 1971), and the major change in diversity corresponds to a steep decline in moisture availability in the central United States. Reptiles also exhibit a westward decrease in diversity (Kiester, 1971) but the gradient is, not unexpectedly, much less steep than that for amphibians: reptiles are, in general, less affected by arid conditions than are amphibians but are more susceptible to increases in harshness (as determined by temperature) than are birds or mammals.

The South American vertebrate fauna offers considerable potential for evaluating this prediction, but distributional data are lacking or rudimentary for most taxa. Available information, however, seems to support the third prediction. Diversity of amphibians (Lynch, 1979), reptiles (Dixon, 1979), and birds (Slud, 1976; Donahue et al., in prep.; Terborgh et al., 1984) is highest along the lower slopes of the Andes and the immediately adjacent lowlands as compared to the lowlands of the Amazonian basin itself. Moreover, as expected, diversity decreases with increasing altitude and a rise in the harshness of montane environments.

Species diversity patterns of plants, to the extent that they have been resolved, parallel the data for vertebrates. Based on current knowledge, and on projections of the numbers of species estimated yet to be discovered and described,

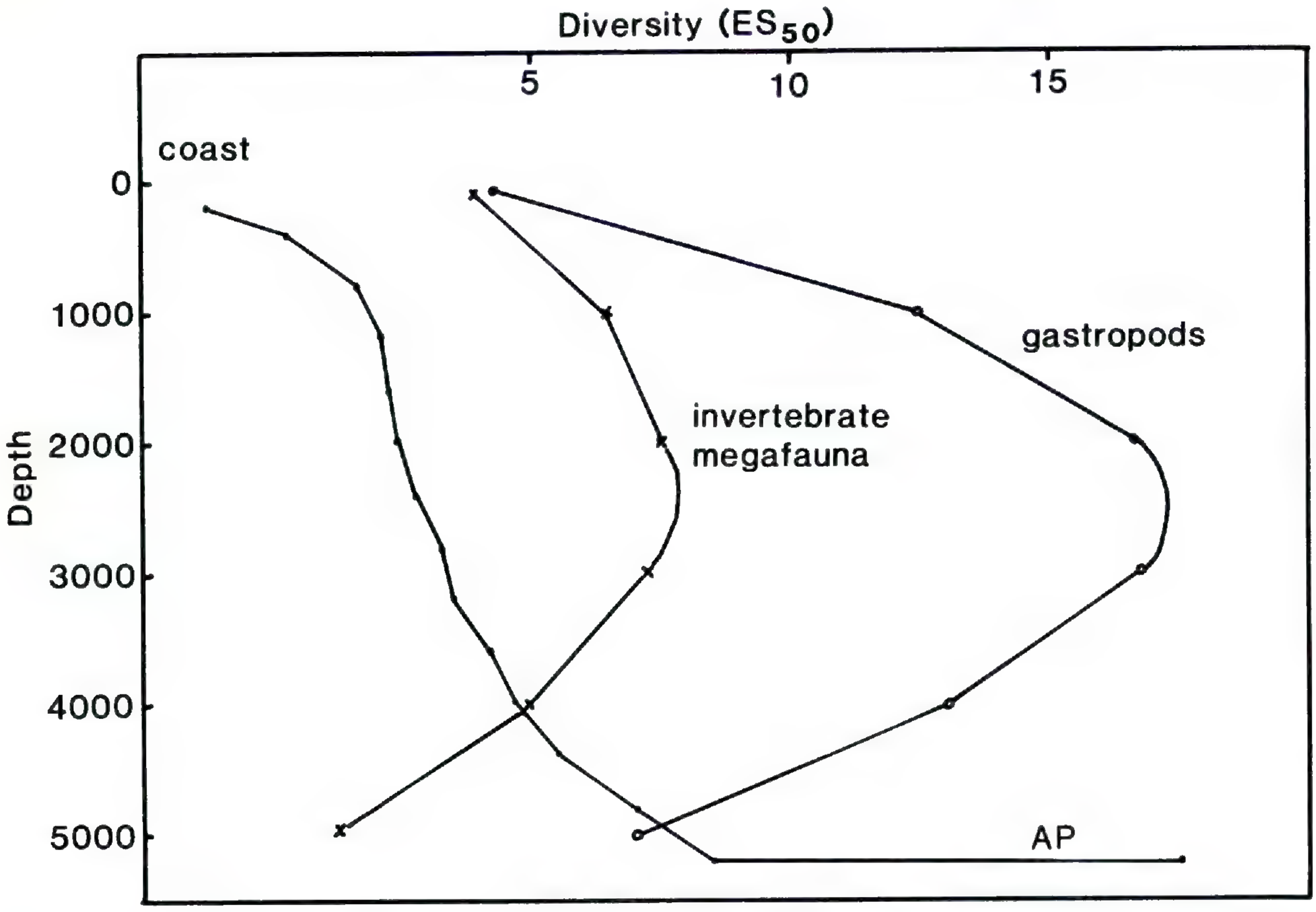

FIGURE 4. A topographic profile of the continental margin in the western Atlantic (at 35°N latitude) plotted with the expected diversity of representative invertebrate groups at the given depths (data from Rex, 1981a). The shape of the two species diversity curves is exemplary of that found in other benthic marine invertebrates. Vertical exaggeration about ×130.

plant diversity appears to be highest along the lower, tropical and subtropical slopes of the Andes when compared to the Amazonian basin (Gentry, 1982b, 1982c; pers. comm.). This must remain a tentative conclusion, of course, but the large number of species with very restricted ranges within the Andes is enormous and even many small mountain valleys harbor large numbers of narrowly endemic species.

Geographic transects of continental species diversity that are appropriate for testing this prediction are scarce and potentially susceptible to influences other than that of lithospheric complexity. Alternative ways of examining the influence of complexity on diversity will be pursued in subsequent predictions.

A further evaluation of the third prediction can be made using data from the marine realm. In this case, longitudinal transects probably exhibit less geographic variation in harshness and thus presumably show fewer effects of extinction than do transects across continents. Three patterns of diversity/complexity are relevant for the third prediction.

a. *North Atlantic diversity gradients.* From the coast, species diversity of benthic invertebrates increases on the continental slope and rise but decreases again as abyssal depths are approached (Hessler & Sanders, 1967; Sanders, 1968; Rex, 1981a). Indeed, diversity is highest for virtually all groups at depths of 2,000–3,500 meters (Rex, 1981a). Much attention has been paid to the causes of high diversity in the deep-sea (see Discussion), but one explanation has not been seriously considered, namely, increased lithospheric complexity.

The slope and upper rise represent the region where continental and oceanic crustal regimes meet. Relative to shelfs, rises, and the abyssal plain, continental slopes are more highly complex geomorphologically, with many deep submarine canyons and gullies generally traversing their flanks (e.g., Uchupi, 1968). The relationship between the continental margin profile of the North American Atlantic coast and two representative diversity profiles for marine invertebrates is pictured in Figure 4. In this figure, the profile itself does not adequately convey the complexity of the slope and upper rise sufficiently because the scale is too small.

It can be hypothesized, therefore, that increased diversity with increasing depth is related

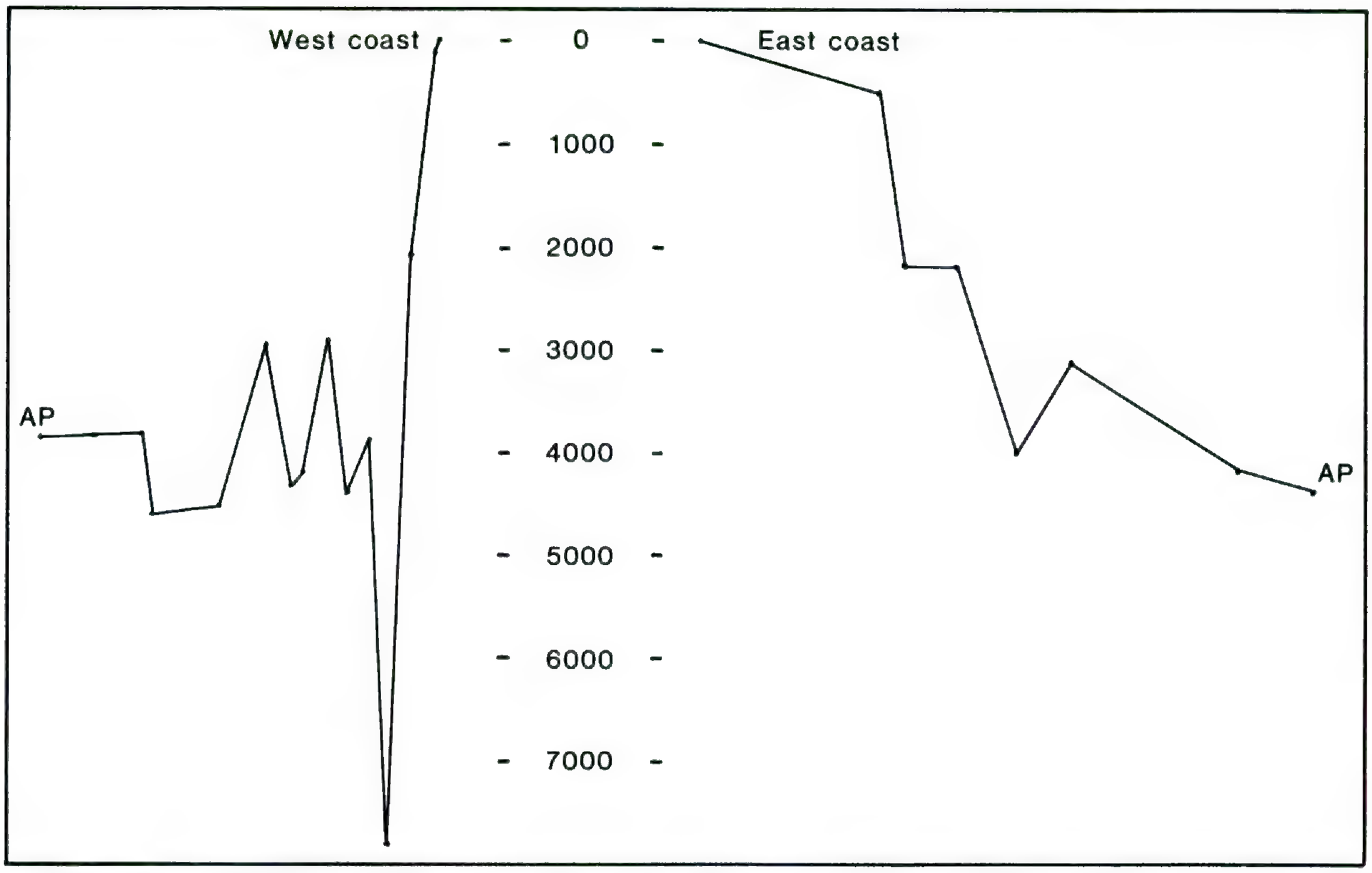

FIGURE 5. Topographic profiles of the Pacific and Atlantic continental margins of South America at 25°S latitude. The profiles begin at the coast and end at the abyssal plain (AP). The Pacific margin is tectonically active and much more complex geomorphologically than the passive margin of the Atlantic. Higher species diversity along the Pacific coast is postulated to result from increased rates of isolation in that spatially more complex region (see text). Vertical exaggeration about ×70.

to gradients in geomorphological complexity and to the opportunities that complexity creates for geographic isolation and differentiation. This hypothesis differs markedly from the prevailing ecological explanations for these diversity patterns such as the time-stability hypothesis, which will be reviewed and analyzed in the Discussion.

b. *Active versus passive plate margins.* Active plate margins such as the western coast of South America are much more complex geologically than passive margins as exemplified by the Atlantic (Fig. 5). Active margins gain their complexity from the extreme structural relief resulting from plate–plate interactions; passive continental margins, in contrast, may even degrade in complexity through time due to the deposition of continental sediments. Consequently, we would predict that active margins, which are continually changing their configuration, should promote higher diversity.

The available data seem to support the prediction. Thus, species diversity of bivalve molluscs is nearly twice as high along the western coast of South America than along the eastern coast (Stehli et al., 1967; Valentine, 1971). This pattern of diversity extends northward to North America but there the pattern is confounded by a Late Cenozoic extinction event in the western Atlantic (Stanley & Campbell, 1981).

c. *Large-scale diversity patterns of the Pacific.* The Pacific basin shows considerable variation in geomorphological complexity, from being the least complex on the abyssal plain of the central Pacific, to very highly complex in the Indo-Australian region where microplates, island arcs, and areas of subduction abound. Using this gradient in complexity as a predictor of diversity, greater diversity would be expected along the western margin of the Pacific. This is precisely what is seen.

The highest diversity of bivalve molluscs, for example, is found in Australasian waters (Stehli et al., 1967), with over 1,000 species as compared to the 150–250 species found in the central and eastern Pacific. Zooxanthellate (Rosen, 1981) and hermatypic corals (Stehli & Wells, 1971) also show greatest diversity in the western Pacific. Stehli (1968) presented data for other groups (e.g., gastropods) having a similar pattern of diversity.

Prediction 4. Large clades, widely distribut-

TABLE 2. Patterns of diversity in neotropical flycatchers (Tyrannidae) and tanagers (Thraupidae).

	Andean Region	Central American Region	Amazonian Region
Relative area	0.27	0.30	1.0
Rank order in geomorphological complexity	1	2	3
Tyrannidae[a]			
Differentiated taxa	310	177	184
Rank order	1	3	2
Differentiated taxa/genus	6.89	4.12	3.76
Thraupidae[b]			
Differentiated taxa	297	123	105
Rank order	1	2	3
Differentiated taxa/genus	9.00	6.15	5.53

[a] Data for the tyrannids from Traylor (1979).
[b] Data for the thraupids from Paynter and Storer (1970).

ed over the same areas, will exhibit covarying gradients in diversity that parallel the gradient in lithospheric complexity.

The third prediction was primarily a statement about gradients of diversity averaged over many clades, that is, a statement about biotic patterns. The fourth prediction partitions that biotic pattern and makes a statement about the causes of diversity within and among the clades themselves.

If a clade is distributed widely over an area that has significant variation in geomorphological complexity, the hypothesis of lithospheric complexity predicts diversity will be higher in regions of higher complexity. But again other causal factors must be held constant, thus we assume that taxa within the clade have been distributed in the different areas for about the same amount of time, and that extinction rates have been roughly equivalent across the entire distribution. If these assumptions are satisfied, then complexity should emerge as the primary predictor of diversity patterns.

In order to examine this prediction, two highly diverse and widespread avian families of tropical America were examined, the tanagers (Thraupidae) and the flycatchers (Tyrannidae). Three biogeographic regions, the Andes (upper part of tropical zone and above), Central America, and tropical lowland Amazonia, were chosen for comparison, with each representing an area of very high, intermediate, and low geomorphological complexity, respectively. Diversity was calculated by tabulating the numbers of endemic subspecies (in the case of polytypic species) or monotypic species in each region, following the recent systematic treatments of the Peters' "Check-list of Birds of the World" (Paynter & Storer, 1970; Traylor, 1979); subspecific, rather than species-level, taxa were ennumerated in order to estimate more accurately the number of differentiated evolutionary units (Cracraft, 1983a).

The results are shown in Table 2. Diversity in both families parallels the gradient in lithospheric complexity. It is also noteworthy that this is especially true even when area is taken into account; diversity is not related to a simple area-effect. Amazonia covers a much greater area, yet contains only about the same number of differentiated taxa within these two families as does Central America. Also revealing is the number of taxa per genus that have differentiated in the three areas. For both families, the Andean region shows the greatest average amount of differentiation per genus, followed by Central America, and then Amazonia.

OTHER RATE-CONTROLS OF SPECIATION

Spatial and temporal variation in lithospheric complexity has been hypothesized above to effect a major control on speciation rates, and thus to contribute significantly to explaining patterns of diversification. Other factors are also widely acknowledged to contribute to variation in speciation rates, and the purpose of this section is to assess their contribution. Not all the evidence for and against these factors will be reviewed here—their existence and potential importance is assumed. Instead, this discussion evaluates whether they might constitute a significant causal mechanism underlying patterns of diversification. It will be argued that, although these factors might influence speciation rates within clades (and in some cases perhaps significantly so), they appear to have had a limited impact on defining major spatial patterns of diversity.

INTERNAL MORPHOGENETIC COMPLEXITY

Differentiation following isolation is a function of the amount of morphogenetic complexity

within the individuals of a species. If those individuals exhibit little or no variation, then the rate-change in character divergence following isolation should be low, and thus too the probability of differentiation (Stanley, 1975, 1977; Wiley & Brooks, 1982). Morphogenetic complexity means the amount of variation as expressed within the developmental pathways of individuals of a population, a notion equivalent to the concept of canalized information as used by Wiley and Brooks (1982). Any changes within the genome that have effects on developmental pathways, and thus on phenotypic expression, are potentially important in establishing the probability that a population will differentiate once it becomes isolated. Thus, variation in morphogenetic complexity within the species of a clade might influence their speciation rate (Cracraft, 1982a): clades comprised of species having high internal complexity should speciate at a higher average rate than clades with less complex species (all things being equal).

Present evidence suggests, for example, that genomic modifications such as gene duplication, polyploidy, and gene rearrangements, in addition to point mutations, can alter developmental pathways and thus adult phenotypes (Wilson et al., 1977). As a consequence, the prediction might be made that if individuals within a clade are characterized by these types of genomic modifications, then the probability of speciation will be relatively high. Wilson et al. (1977), in fact, proposed that speciation rates in mammals have been higher than those for anurans partially because of a higher rate of chromosomal change in the former. Levin and Wilson (1976) made a comparable claim to explain patterns of diversity within angiosperms.

Properly designed comparative studies should give us much more insight into the causal relationship between large-scale genomic change and speciation rates within and among clades. If this relationship proves significant, the question will arise as to how that might be relevant at the level of diversity gradients within biotas. At first glance, it might appear difficult to conceive of numerous clades exhibiting congruent patterns of genomic modification among their species, yet such geographic gradients have been suspected for some time. The incidence of polyploidy, for instance, increases with increasing latitude (Grant, 1971); what effect that has had on geographic variation in speciation rates is a separate, as yet unanswered, question.

BEHAVIORAL-ECOLOGICAL ATTRIBUTES OF SPECIES

Biologists have long hypothesized a causal connection between certain behavioral-ecological attributes of species and the likelihood that they might speciate. Unfortunately, conflicting predictions or expectations are common. Substantial literature suggests that ecological generalists (or eurytopes) would be more likely to colonize distant habitats, become isolated, and differentiate, than would specialists, or stenotopes (see Parsons, 1983 for a summary; also Kohn, 1971; MacArthur, 1972; Diamond, 1975, among many others). Yet, stenotopy, rather than eurytopy, has been hypothesized to lead to speciation through small, ecologically restricted populations (Jackson, 1974; Eldredge & Cracraft, 1980; Vrba, 1980, 1983). The best available data supporting this latter hypothesis are those of Jablonski (1982; see also Valentine & Jablonski, 1983), in which gastropods and brachiopods with nonplanktotrophic larvae (stenotopes) presumably speciate at higher rates than those with planktotrophic larvae (eurytopes).

While it seems clear that possession of certain ecological or behavioral characteristics may help determine the probability of speciation for species within a clade, this can translate into geographic patterns of diversity only if the characteristics themselves vary geographically, if they vary in the right direction, and if the different clades of organisms comprising the biota being investigated show covarying sets of characteristics when displayed geographically. Such a conjunction of events suggests this would occur only very rarely, and consequently this category of speciation rate-control probably has little influence on geographic diversity gradients.

SEXUAL SELECTION

Fisher (1930) proposed that a genetic correlation between assortative mating created by female choice, on the one hand, and secondary sexual characteristics of males (the basis for the choice), on the other, can lead to rapid evolutionary change within populations. Lande (1981, 1982) and West-Eberhard (1983) have also argued that such "runaway" sexual selection might be responsible for high rates of speciation in some groups.

In theory, this mechanism for rapid divergence might be potentially important in those groups of organisms possessing the appropriate mating

systems (West-Eberhard, 1983). Yet, an upper-level constraint on this process of divergence would still exist and include those factors controlling the rate of geographic isolation; in most cases, sexual selection itself could influence the rate of divergence only after populations became isolated.

The influence of sexual selection on speciation rate thus remains highly speculative. Unless the incidence of sexual selection varies geographically—e.g., if sexual selection were more frequent in highly diverse ecosystems (as perhaps is the case)—then its contribution to establishing geographic gradients in diversity would be minimal. Even if this geographic variation existed, however, speciation would not be expected to occur faster than the rate of geographic isolation.

The Rate-Control of Extinction

Despite a large literature, biology still lacks a widely accepted deterministic theory of extinction. Emphasis has been placed on the occurrence and explanation of short-term pulses (so called "mass" extinctions) rather than on the patterns and processes of normal "background" extinction. Another factor mitigating against the development of a theory of extinction has been the difficulty of testing any proposed hypothesis. The analysis of causation within extinction theory is particularly susceptible to scale effects: at one level climate may change, thereby initiating numerous environmental consequences leading to extinction, but at the same time that extinction also can be examined causally at the more "proximate" level of processes within populations.

At issue here are patterns of extinction calling for explanations at hierarchical levels above that of populations. Such patterns are taxonomic, at the level of clades, and biotic, at the level of assemblages of species, or some combination of both. Thus, taxonomic patterns of extinction within or among clades can be expressed either geographically or temporally at a single location. Patterns of extinction within biotas are statistical summations of extinction within and among clades. Within a biota, changes in extinction rate are expressed temporally, whereas patterns between biotas can be both temporal and geographic.

These large-scale patterns, above the level of populations, can be expected to have first-order causes which themselves are expressed at a hierarchical level above that of populations. It is proposed here that change in the temporal and geographic gradient of environmental harshness (favorableness) is the primary control of extinction rates, and thus of the large-scale extinction patterns just mentioned. This hypothesis will be developed in more detail now and later will be compared with other potential rate-controls of extinction.

The Hypothesis of Environmental Harshness

The twin concepts of environmental harshness and favorableness have been discussed extensively in the ecological literature (especially Andrewartha & Birch, 1954). Most of that literature relates harshness with density-independent population regulation (see Enright, 1976 for a discussion of how harshness might function within a density-dependent context). The hypothesis presented here expands that thinking to account for large-scale gradients in extinction.

Premise 1. Individual organisms (and thus populations and species) possess a definable physiological capacity permitting them to exist within a specific environmental regime; no organism or species can live in all environments.

Premise 2. As the physical characteristics of an environment shift away from the "optimal" conditions for a species, the intrinsic rate of increase declines and eventually becomes negative, resulting in extinction of the population.

In this case, we define "optimal" in terms of the conditions (narrow or broad) at which the rate of increase is at or near maximum, but other measures could also be chosen. This premise has considerable empirical support, and physical attributes of the environment are known to influence physiological functions, which in turn have effects on demographic parameters such as fecundity, survivorship, age of reproduction, among others (Andrewartha & Birch, 1954; Ricklefs, 1973; Krebs, 1978).

Premise 3. The environments of the earth can be arranged along a scale defined in terms of their harshness/favorableness relative to the mean physiological tolerances of a random sample of the world's organisms.

Many physical parameters have the potential to influence the survivorship and reproductive capabilities of organisms. Moisture and temperature gradients are generally acknowledged to exert a greater overall effect than do other parameters, and that assumption is adopted here. Therefore, the premise states that, in principle,

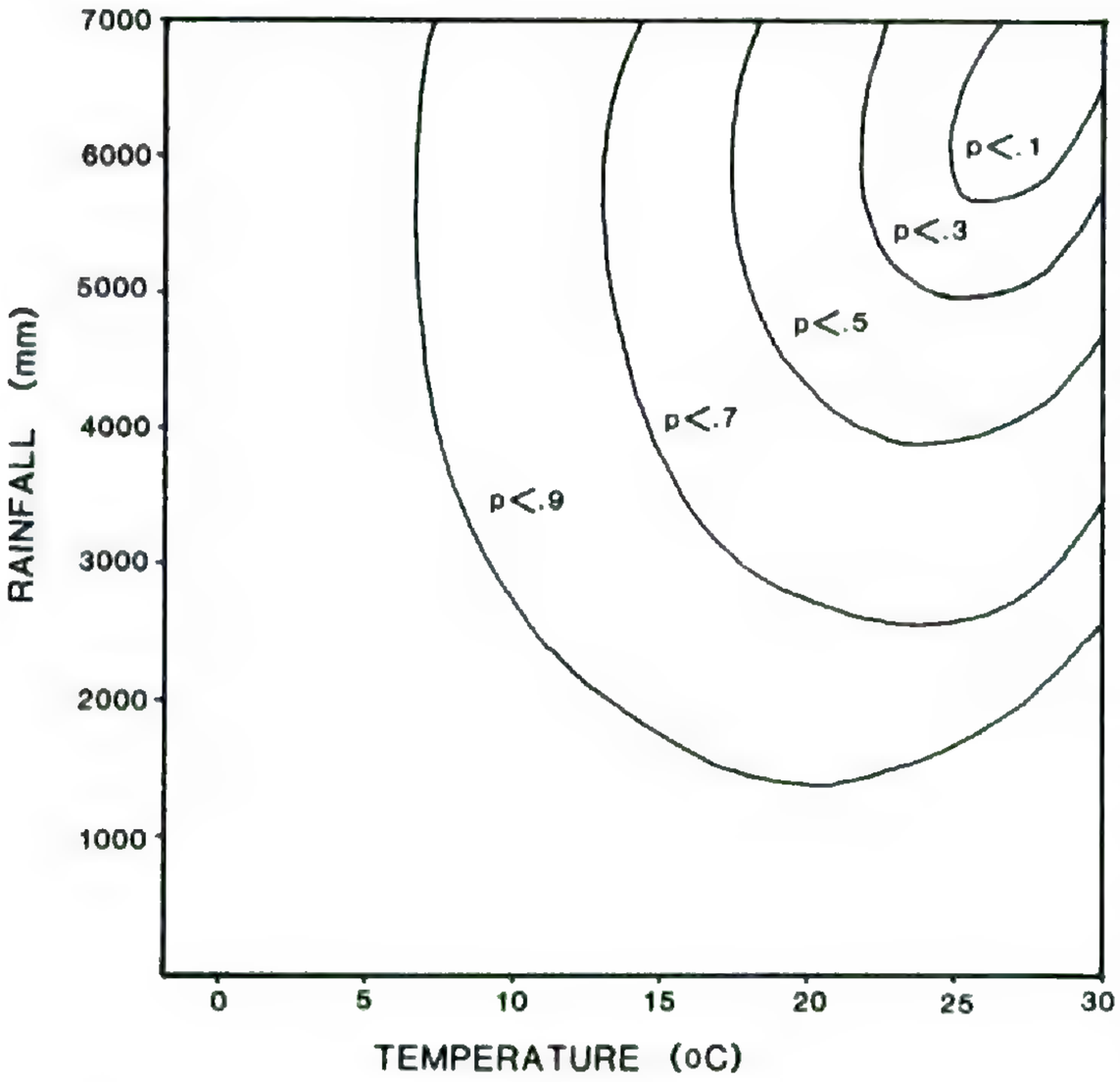

FIGURE 6. A theoretical diagram postulating a relationship between the probability of extinction and the position of a population in a space of environmental harshness/favorableness, as measured in terms of mean annual rainfall and temperature (modified after Birch, 1953 and Krebs, 1978).

the joint influences of temperature and moisture on the intrinsic rate of natural increase can be experimentally determined for each species (e.g., the classic study of Birch, 1953), and a measure of that influence (harshness/favorableness) can be mapped geographically.

Premise 4. The frequency of species occurrences along the harshness/favorableness scale is decidedly nonrandom.

Also having much empirical support, this premise merely states that environmental extremes in temperature and/or moisture are tolerated by relatively few organisms. In areas of low harshness (generally speaking, in environments that are warm and moist; see below), organisms require less energy to maintain physiological homeostasis relative to their surroundings than do organisms in harsher environments.

These premises yield the following hypothesis: *the probability of extinction is a function of the change in the value of environmental harshness to which a species is exposed* (Fig. 6).

The hypothesis makes more explicit what biologists have intuitively recognized for many years. But it also makes a larger claim not often recognized: that taxonomic and biotic patterns of extinction are *primarily* a function of spatiotemporal changes in environmental harshness. Ecologists have long proposed a relationship between environmental harshness/favorableness and diversity (e.g., Richerson & Lum, 1980), but most of these discussions have not pinpointed the causal connection of this relationship: that is, harshness influences only *one* component of diversification, namely extinction rate (see Connell, 1975 for a discussion of the ways in which harshness gradients influence community structure).

Extinction rates are exceedingly difficult to study because their analysis is more dependent on the quality of the fossil record than is the analysis of speciation rates. For example, if we compare Recent sister-clades differing greatly in diversity, the minimal number of speciation events for each clade can be specified (N-1, where N is the number of species) even in the absence of a fossil record; relative rates can thus be estimated directly. On the other hand, a comparable statement regarding the number of extinctions in each lineage is not possible in the absence of a fossil record. A method must be found to document the loss of a species, not its mere presence, and a historical record is our only way of doing this.

Measurements of extinction rates based upon an analysis of the fossil record entail additional difficulties in that paleontologists rarely use species-level taxa but often are compelled instead to study taxa at the generic or family levels, precisely because of the lack of detail in the fossil record. Unless the supraspecific taxa contain the same average number of species (and with little variance), however, comparisons among them will not yield accurate statements about the relative amounts of extinction at the relevant evolutionary level, namely that of species.

Evaluation of the hypothesis of environmental harshness not only relies upon the fossil record for an estimation of relative rates of extinction, but also for the measurement of changes in harshness through time. The components of harshness, here considered to be temperature and moisture, are retrievable from both paleontological data and from physical and chemical characteristics of the rock record itself. Unfortunately, detailed study of the relationship between extinction rate and harshness calls for a well-preserved historical record, which is usually lacking for terrestrial environments. Despite its inadequacies, paleontology can provide, nevertheless, abundant data at a coarse-grained level with which to evaluate the hypothesis of environmental harshness.

A major prediction of this hypothesis is that as a specific environment becomes harsher, the average extinction rate of the component species of the biota will rise. As defined earlier, harshness increases as temperatures and moisture approach extreme values. Under these conditions, more organisms become physiologically stressed, population sizes decline, and the probability of extinction increases. Paleontologists have documented numerous cases of increases in extinction rates accompanying climatic shifts toward harsher environments (Axelrod, 1967). For example, the marked increase in elevation of the Andes in the middle to late Cenozoic resulted in a change toward extreme aridification along the west coast of South America, thereby causing a once diverse biota to become extinct and be replaced by one much less so (Berry, 1938). A widespread, relatively diverse biota disappeared in North Africa as the climate became more arid in the late Cenozoic (Moreau, 1952, 1966). Similar changes in moisture and extinction gradients also took place in Australia (Kemp, 1981; Galloway & Kemp, 1981).

Increases in harshness as measured by temperature are also known to have increased extinction rates. Hickey (1981, 1984) reported a gradual increase in the extinction rates of floras as global temperatures became cooler across the Cretaceous-Tertiary boundary. Furthermore, extinction rates were higher in higher latitudes where the temperature gradient was steeper. That deviations in temperature away from physiologically more favorable regimes increase extinction rates of floras has been noted by many workers, and perhaps the classic example is that associated with the Pleistocene climate fluctuations (e.g., Axelrod, 1967; Kershaw, 1981). Finally, in the marine realm, temperature change is also strongly implicated in large-scale extinction events (Stanley, 1984; Kauffman, 1984).

That large-scale, geographic increases in environmental harshness result in concomitant responses in the steepness of extinction gradients can scarcely be denied, yet this does not inform us about the relative role of increased harshness, when compared to other postulated causes of extinction, in effecting a control over patterns of diversification. At the level of biotas, changes in harshness seem to play an important part in the evolution of geographic patterns of diversity, but their relative contribution to controlling patterns of diversity, within and among clades is somewhat more difficult to establish because a relatively extensive fossil record is required. Most clades are distributed nonrandomly and so global changes in harshness should alter extinction rates of clades nonrandomly (e.g., as in latitudinal gradients). Changes in harshness, however, often result from relatively local tectonic evolution, and thus patterns of extinction within clades might exhibit a "stochastic" appearance over a large geographic area (i.e., clades would go extinct, in this case, purely as a result of being in the wrong place at the wrong time).

Many clades show a pattern of reduction diversity during their history, but the causes of this common pattern have not yet been analyzed comparatively. Unfortunately, it is not possible at this time to evaluate the generality of the environmental harshness hypothesis by reference to a large suite of phylogenetically controlled data. As an alternative, we can undertake a partial evaluation by examining other postulated causes of extinction and assessing their potential for explaining both intracladal and geographic patterns of biotic diversity.

a. *Tectonic elimination of habitats.* Tectonic activity brought about by lithospheric plate motion directly obliterates habitats (e.g., shallow and deep-water marine environments during continent–continent collisions) or changes in their extent through mountain building, alterations in sea-level, or volcanism (Valentine & Moores, 1970, 1972; Valentine, 1971, 1973; Schopf, 1974; Bakker, 1977; Hallam, 1981; Axelrod, 1981). Tectonic events can have major effects on the extinction patterns of local biotas, and generally are recognized to contribute to mass extinctions. In particular, if these events have a large geographic scale, then they can alter patterns of diversity within higher taxa (examples can be found among the major Phanerozoic mass extinction events). Whether tectonic events are a major, direct control on long-term patterns of reduction diversity within clades is questionable, although marine regressions and transgressions can span many millions of years and might alter diversity gradually.

Tectonic activity per se is thus not likely to be the principal causal agent of most geographic gradients in extinction or of long-term patterns of reduction diversity (particularly within terrestrial organisms). But tectonic alterations of environments play a significant role in geologically "short-term" mass extinctions, and thereby could leave their signature on "long-term" patterns of diversity within clades. The extent to which these

geological events could help explain congruent changes in diversity over many clades would depend upon the magnitude of the events themselves, their location, and the clades of organisms that happen to be exposed to them.

b. *Competition.* Ecologists have long identified competition as a major cause of extinction within populations, and the tradition goes back to Darwin himself. Paleontologists and others interested in large-scale patterns of diversification have adopted many ecological ideas regarding competition and its role in extinction and have reified them as patterns and processes among higher taxa. A common application of this thinking occurs when one group of organisms is said to "replace" another, trophically similar group over a period of time (perhaps many millions of years). Well-known examples ascribed to competition include the replacement of creodonts by condylarths (Simpson, 1953), South American marsupials by North American placentals (Simpson, 1950), multituberculates by primitive placentals (Simpson, 1953; Van Valen & Sloan, 1966), dinosaurs by placental mammals (Van Valen & Sloan, 1977), and even invertebrates by primitive gnathostome fishes (Thomson, 1977), to name only a few. If the causal assessment of these replacements is correct, then by implication competition would be a major factor leading to reduction diversity within clades.

None of these putative examples is well documented, however, at least by the standards currently acceptable within modern ecology (Wiens, 1977; Connell, 1975, 1980, 1983). Many difficulties arise, first in recognizing the mere presence of competition within Recent communities, and then, second, in determining that it is an important force controlling the relative abundances of species within those communities. To extend this type of analysis to fossil communities magnifies these difficulties to a point at which the problems become intractable. Showing that one species competitively replaces another requires extensive ecological analysis; arguing that many species of one clade (or one biota) can competitively replace many species of another clade or biota requires detailed data that a fossil record is incapable of supplying. The "replacement" can be documented, but a causal hypothesis of competition cannot.

The proposition that competition is a major factor controlling extinction rates and thus shaping patterns of diversity is unsupported. We could reach this conclusion, moreover, *even accepting* the hypothesis that competition is ubiquitous and important in the regulation of species abundances within local communities. But given that this latter hypothesis is still being debated within ecology, it seems premature, and perhaps presumptive, to conclude that competition is a major causative agent of extinction either within clades or between biotas (see Gould & Calloway, 1980, for an analysis of the "classic" brachiopod-to-clam replacement, which they conclude resulted from the Permian extinction event not competition).

c. *Predation.* Predation is postulated to be an important factor in regulating relative abundances within populations. Depending upon the ecological system being studied, the presence and effect of predation may or may not be easily determined. Within paleontological assemblages, predation has been investigated most extensively in marine invertebrates in which evidence is often obtained directly from the fossils themselves. These studies suggest the possibility that predation pressure has increased the extinction rates in some clades or organisms. Stanley (1977), for example, postulated that the post-Paleozoic increase in the frequency of shelled infaunal bivalves as compared to exposed epifaunal forms was the result of more intense predation on the latter. This "species selection," Stanley (1977: 238) proposed, led to higher extinction rates of epifaunal species and major changes in diversity within and between clades. Likewise, Stanley (1977) attributed the post-Late Mesozoic decline of articulate brachiopods to increased predation from teleost fish, snails, and crabs.

The significance of predation within ecosystems cannot be denied, yet acceptance of its importance as a causal agent controlling rates of extinction is less warranted. Under most natural conditions, predators do not extirpate their prey, although at times they may affect their numbers substantially. If predation does not cause extinction of a prey species directly, population sizes might be so reduced that extinction could occur stochastically or via other agents. Predation might be expected to play a role in species extinction in communities with simple structure in which prey species cannot (or have failed to) develop any effective means of predator avoidance. In contrast, if prey species are widely distributed or have high dispersal abilities (or are unavailable to predators) during some part of the life cycle, then the probability of extinction via predation would be expected to be relatively low.

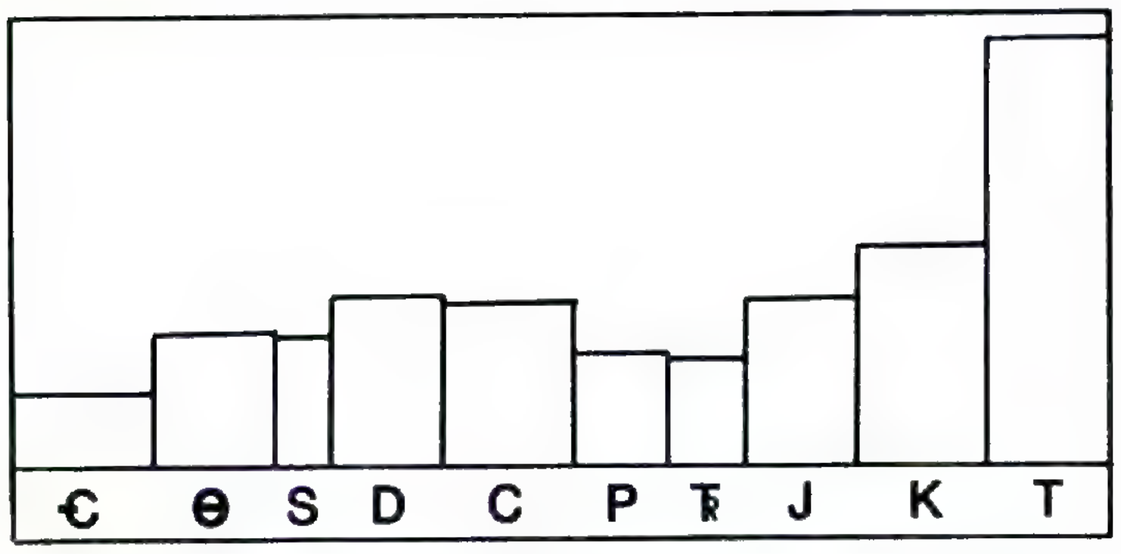

FIGURE 7. Phanerozoic species diversity curve for marine invertebrates showing a marked rise in diversity in the Cretaceous and Tertiary (after Raup, 1976a and Sepkoski et al., 1981).

As a consequence of these factors, predation will probably not be an effective mediator of extinction rates in most groups of organisms. Any hypothesis that predation is important needs to be critically evaluated and thoroughly documented.

d. *Behavioral characteristics.* The degree of behavioral-ecological plasticity of species has been postulated to influence the probability of extinction. Jackson (1974), Eldredge (1979), Eldredge and Cracraft (1980), and Vrba (1980) have suggested that eurytopic species will be less likely to go extinct than stenotopes. Eurytopic species tolerate a relatively wider range of environments, and are thus assumed to be more widely distributed and have larger overall population sizes than stenotopes. Extinction rates are postulated to be higher in stenotopes because of their smaller, more narrowly distributed populations.

The correlations (e.g., Vrba, 1980) between eurytopy and clades of low diversity, and between stenotopy and clades of higher diversity, are not easily interpreted. Stenotopic species presumably have higher probabilities of both extinction and speciation; in such cases, therefore, high speciation rates would be postulated to override high extinction rates. Eurytopic species, in contrast, are assumed to be characterized by both low extinction and low speciation rates. If eurytopic clades are generally characterized by low diversity, then that would probably result from the low speciation rates and not low extinction rates, which should instead promote high diversity. Consequently, this suggests that stenotopy and eurytopy, to the extent that they influence intracladal diversity, do so through the mediation of speciation rates and not through effects on extinction.

The preceding discussion makes clear the complex causation underlying extinction rate-controls. Any temporal change in diversity that is attributable to extinction rather than speciation almost certainly will be a manifestation of different causal processes operating simultaneously. Accepting this, we should seek to identify the relative contributions of each cause to the extent possible. In most cases, the available data probably will not permit us to discriminate much more than one or two main factors.

The evidence reviewed here suggests that intracladal patterns of reduction diversity and geographic gradients of diversity, insofar as they reflect variation in extinction, are generally the result of gradients in environmental harshness. This claim is merely one of frequency. Many kinds of tectonic activity can alter extinction rates of biotas on a local scale or sometimes even over areas of considerable extent. Behavioral attributes such as eurytopy and stenotopy have the potential to influence extinction rates, although because they can also affect speciation rates, their analysis is complicated and their role in extinction is questionable. In principle, competition and predation, through their effects on species abundances, might contribute to regulating the probability of extinction but, once again, the analysis of this contribution is exceedingly difficult, if not impossible, in most situations. Moreover, even though populations might be subject to these presumed density-dependent interactions, density-independent factors might actually be the primary controls on mortality (Enright, 1976). The conclusion is that only environmental harshness is likely to constitute a significant influence on the types of extinction patterns considered here. Because of its pervasive, and well-documented, influence on extinction, the effects of environmental harshness should be eliminated prior to considering other causal hypotheses. Such a procedure will ensure that those hypotheses are evaluated under the best possible circumstances.

DISCUSSION

WHAT IS THE SHAPE OF THE PHANEROZOIC DIVERSITY CURVE?

The Phanerozoic diversity curve has been the subject of much discussion over the past decade (Valentine, 1972; Raup, 1972, 1976a, 1976b; Bambach, 1977; Sepkoski, 1978, 1979; Sepkoski et al., 1981; Signor, 1982). Arguments have centered on the empirical shape of the curve itself, in particular whether diversity has been at equilibrium since the end of the Paleozoic or whether

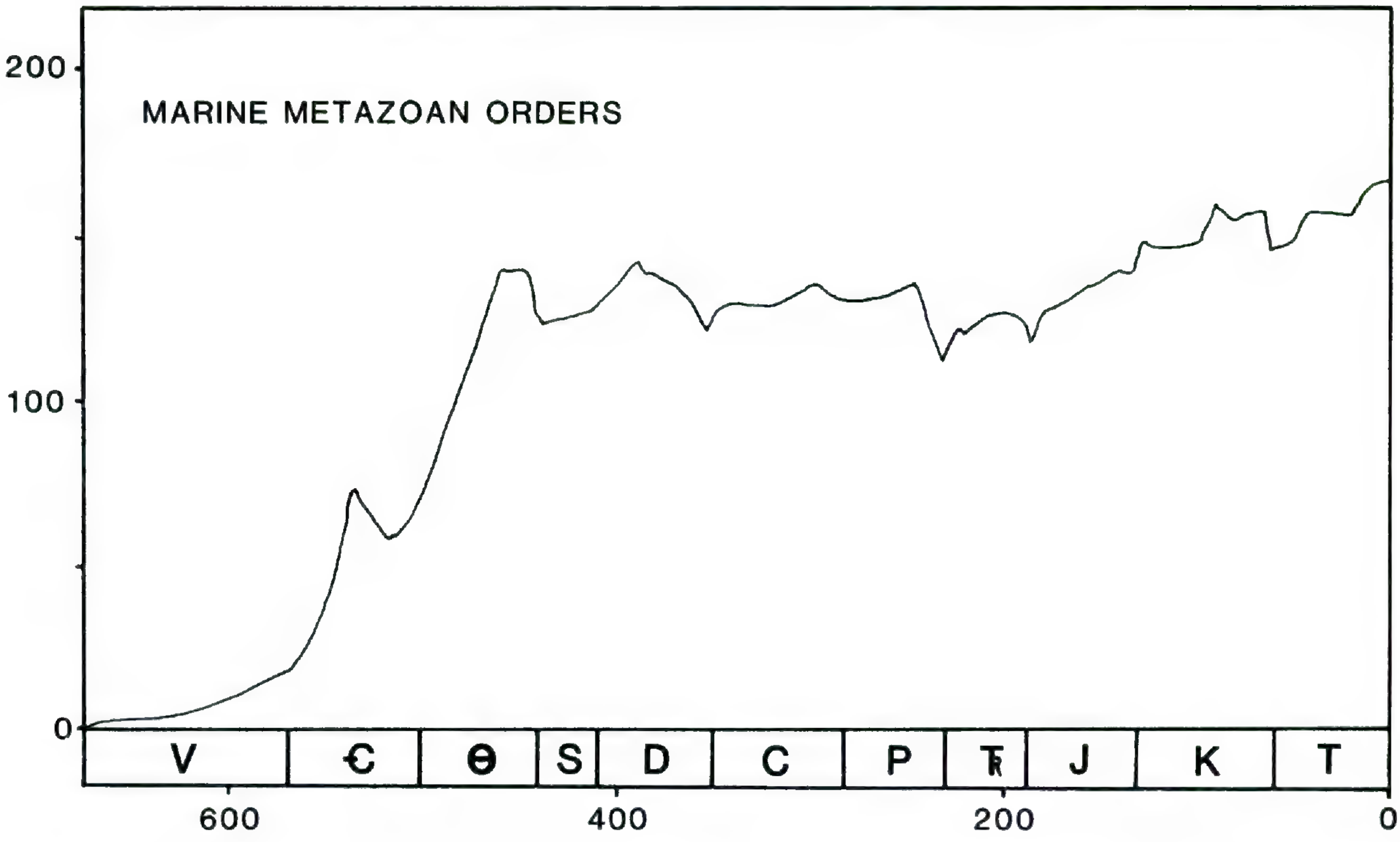

FIGURE 8. A Phanerozoic diversity curve for marine "orders" of Metazoans (from Sepkoski, 1978). Curves such as this have been used to support the hypothesis that diversity has been in equilibrium since the late Paleozoic.

there was a late Mesozoic-Cenozoic rise. Various authorities now generally agree that present data show a curve for marine invertebrates that rises abruptly from a Cambrian low to one of apparent equilibrium through the Permian, followed by a dip in the Triassic, and a subsequent increase in the late Mesozoic and Cenozoic to levels that were four to eight times those of the Paleozoic and early Mesozoic (Sepkoski et al., 1981; Signor, 1982; Fig. 7).

Our concern here is not with the actual empirical shape of the curve but with its expected shape given specific models of diversification. With respect to the former, one might argue that available data, which are primarily of marine organisms, are inadequate to test any of the curves that might be predicted. For one thing, a meaningful evaluation of the pattern of diversification cannot be restricted solely to marine taxa (e.g., Sepkoski et al., 1981), because many of them also have radiated into nonmarine environments. Consequently, although the marine pattern is of interest in its own right, most workers would probably agree that it cannot be the benchmark of the Phanerozoic curve itself. Restriction of an analysis to one biotic association (marine, arboreal, terrestrial, freshwater) is only a partial sample of the results of diversification; none of these ecological subdivisions is a closed system as far as diversification is concerned.

Furthermore, estimations of the shape of the diversity curve based on counting supraspecific taxa are inherently biased and inaccurate (Cracraft, 1981b, 1982a; Novacek & Norell, 1982; and earlier discussion). Higher taxa are not equivalent in terms of age, nor does a temporal comparison of their numbers necessarily reflect an accurate comparison of the numbers of evolutionary units within those taxa.

Finally, the Phanerozoic record for freshwater and terrestrial environments is much too poor to provide an accurate estimate of the numbers of species from one time period to the next. As a simple example, the estimated number of *living* arthropods increased tenfold (to perhaps 30–40 million species) in the last few years after it was realized just how diverse the tropical forest canopy is (T. L. Erwin, 1982; pers. comm.). Tropical invertebrate faunas, in general, are still virtually unknown. Given the fact that the most highly diverse biotas (i.e., those that are tropical) are amongst the most poorly preserved in the fossil record, accurate estimates of diversity based on that record should not be expected.

To summarize, we can only praise the efforts of those who have attempted the arduous task

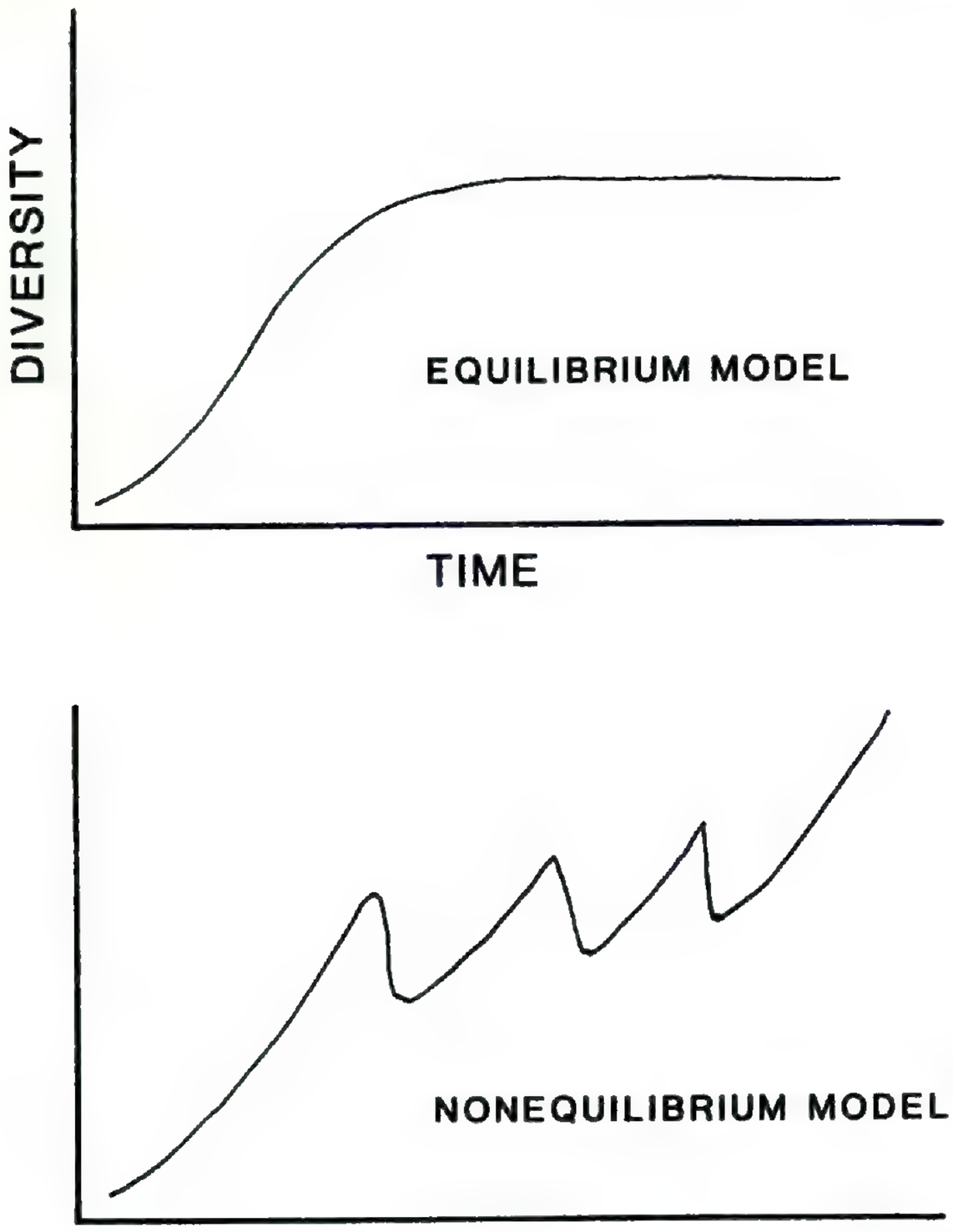

FIGURE 9.—A. Curve illustrating the equilibrium model of biotic diversification. Perturbations such as mass extinctions depress the curve temporarily but diversity eventually rebounds to or near the equilibrium level.—B. A nonequilibrium model of biotic diversification. An intrinsic exponential increase in diversity is expected with the rate of increase constrained by worldwide patterns of environmental harshness/favorableness. Major perturbations such as mass extinctions are postulated to "reset" the curve (see text).

of compiling patterns of diversity from the fossil record, and their emphasis on the marine fossil record is readily understandable. The message here is merely that some skepticism is necessary regarding what these curves actually tell us. They may reveal an accurate picture of diversification patterns within the marine realm itself, yet clearly that record does not depict actual patterns of diversification of all those clades within the biosphere as a whole.

Consequently, the question can be asked: what might be the expected shape of the Phanerozoic diversity curve? Investigators of marine diversity have often assumed the marine environment to be a closed (or semi-closed) system, and the diversity curve therefore to be logistic, or equilibrial (Sepkoski, 1978, 1979; Figs. 8, 9A). Within such a system, perturbations such as mass extinctions depress the curve, but diversity eventually rebounds to the equilibrial value. Only minor variation above equilibrial values would be expected.

If diversification is controlled significantly by lithospheric evolution, isolate formation would be some exponential function of the rate of barrier formation (Cracraft, in prep.). Diversity, therefore, would increase through time. But the path of the diversity curve is constrained by extinction, including both mass and the background rate. In this model, mass extinctions "reset" the curve of diversification, not perturb it from an equilibrial value (Fig. 9B), and changes in the background rate of extinction—as would occur, for example, during periods of global cooling or warming—operate to calibrate the exponential rise function.

Ecologically, a diversity-independent diversification model would not entail a saturation of the resource-space of the biosphere. Indeed, in the absence of external constraints (extinction), that space should grow through time. When differentiation produces new species, it also produces taxa having new (or modified) ways of utilizing the physical and biotic space of the biosphere. Because different trophic levels of a biota have different relative abundances, repeated vicariance of that biota might be expected to yield different diversification rates within each trophic level: we would predict, for example, that the primary consumer (herbivore) level would increase at a higher rate than the secondary consumer (carnivore) level. This may explain the inordinately high numbers of herbivores in systems that have experienced relatively few extinction events over time (e.g., terrestrial environments in the tropics as compared to temperate regions; see below).

Empirically, the Phanerozoic diversity curve seems to fit the diversity-independent model more closely than an equilibrial model. Sepkoski et al. (1981) and Signor (1982) document a precipitous rise in marine diversity since the Triassic, exactly what might be expected given the absence of a major mass extinction during that time (only two "intermediate" events are recorded in the marine record; Sepkoski, 1982). Because this rise is so far above the Paleozoic "equilibrium" level, an equilibrial model cannot easily explain it, whereas the diversity-independent model can.

The hypothesis that Phanerozoic diversity was at some equilibrial value from the Ordovician to the end of the Permian (almost 250 Ma) is also open to challenge and to the claim that di-

versification could have been nonequilibrial (Ross, 1972). First, two significant extinction events, the Ashgillian in the late Ordovician and the Frasnian in the middle to late Devonian (Raup & Sepkoski, 1982), can be hypothesized to have "reset" the diversification curve of the marine biota of the time. Second, although marine diversity appears reasonably constant from the Carboniferous until the end of the Permian, many other groups were apparently radiating into terrestrial and freshwater environments at that time: e.g., amphibians (Carroll, 1977), conifers (Florin, 1951). These groups are underrepresented in calculations of the Phanerozoic species diversity curve.

Finally, the Permo-Carboniferous was a period of harsh global climates (Frakes et al., 1975; Olson & Vaughn, 1970), which can be postulated to have constrained diversification. If true, then the expected exponential rise might have been "damped," thus contributing to the appearance of a diversity equilibrium.

Insufficient evidence thus exists to conclude that Phanerozoic diversity has exhibited an overall pattern of equilibrium. Moreover, there is little reason to expect that speciation and extinction are diversity-dependent (Cracraft, in prep.). The expectation of equilibrium, which has been so widely accepted within the paleontological community, has arisen from an acceptance of only one view within contemporary ecology regarding population regulation and from the assumption that processes at the hierarchical level of clades and biotas are simple extrapolations of ecological processes within and between populations. As these latter processes do not appear to constitute first-order determinants of speciation or extinction, that extrapolation is probably not valid.

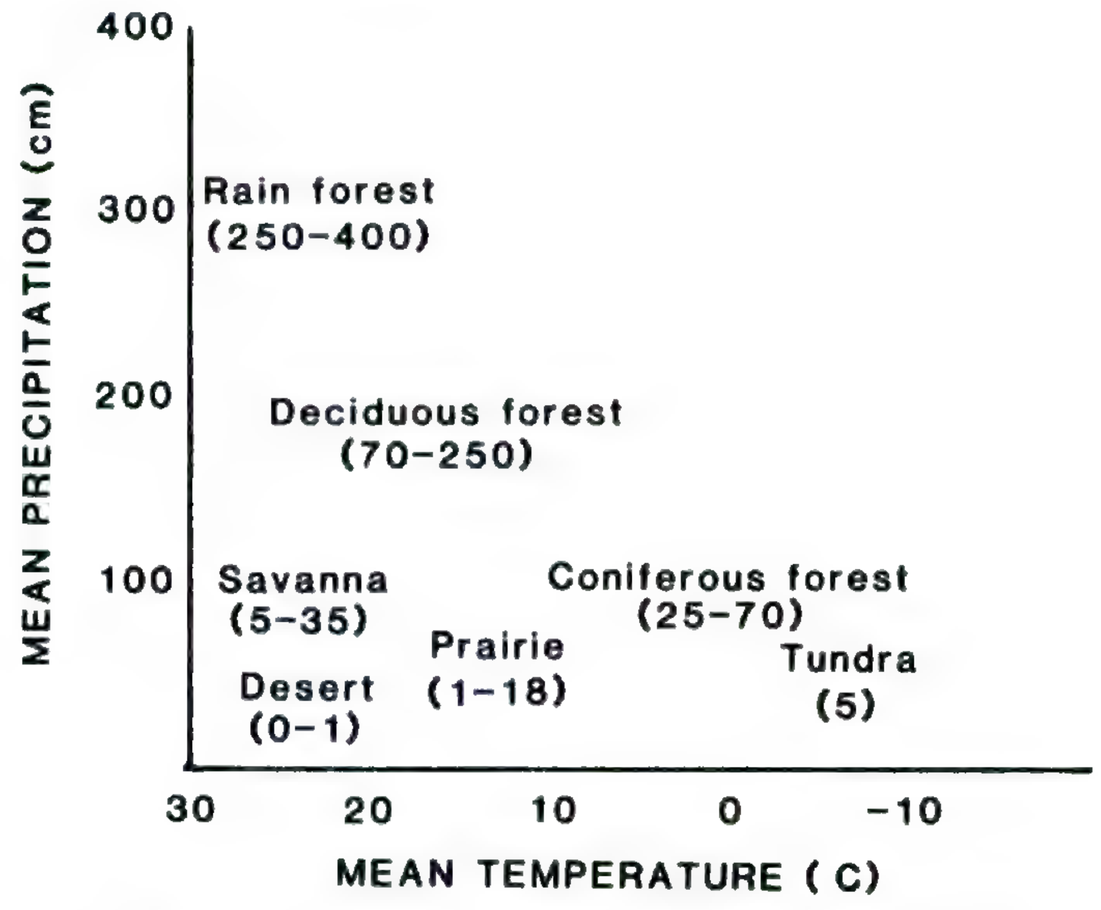

FIGURE 10. Biomass production (tons/hectare) of different vegetational associations relative to a gradient in environmental harshness/favorableness, as measured by mean annual temperature and precipitation (after Smith, 1980). Potential biomass production is constrained by worldwide patterns of environmental harshness (see text).

IS THERE AN UPPER LIMIT TO DIVERSITY?

Acceptance of the idea that biomass has attained an equilibrial value within the biosphere has been the basis for concluding there exists an upper limit to diversity (MacArthur, 1965, 1969; Margalef, 1972; Levinton, 1979). The previous discussion, however, has questioned the underlying assumption of a limit to the evolution of biomass, and that viewpoint will be amplified here (see also Benton, 1979; Cracraft, in prep.).

As long as the biosphere is an open thermodynamic system (Ulanowicz, 1980), the influx of energy and matter will continue to be captured by organisms, ultimately through the processes of reproduction and ontogeny, with biomass thus increasing. Degradation of the earth by chemical and physical processes, and also by organisms, releases matter, some of which is incorporated into living organisms. Incoming solar energy is transduced and used to manufacture organic material, yet only a very small portion (1% or less; Krebs, 1978: 522–524) of the available energy is utilized. Given these observations, then, an increase in biomass would appear to be inevitable, unless some extrinsic factor can be shown to constrain the flow of energy and matter.

Ecologists have often viewed the evolution of biomass and diversity as being tightly coupled so that there is an inverse relationship between diversity and relative abundance. In a biomass-limited world, such an assumption is logically compelling. Still, the evolution of diversity could be related to the evolution of biomass in yet another way. The flux of energy and matter through individuals and populations is the motive force for ontogenetic and evolutionary differentiation (Wiley & Brooks, 1982; Brooks & Wiley, 1984). Thus, diversification takes place as a consequence of biomass expansion. Moreover, as long as energy flow through the lithosphere continues to drive its evolution, taxonomic differentiation will persist unabated.

But are there no limits to biomass evolution? Biologically more meaningful, perhaps, is to speak of constraints on biomass evolution within the

context of a nonequilibrium increase (Ulanowicz, 1980). Through the history of life the most important constraint has probably been a steep gradient in environmental harshness. On the earth today, for example, climates of harsh temperature and moisture regimes restrict net primary productivity (Fig. 10). This observation also implies that space itself has not been a limiting factor of global biomass production. At any one location, however, biomass production could be limited by a variety of factors, abiotic or biotic.

ECOLOGICAL EXPLANATIONS AND THE ANALYSIS OF LARGE-SCALE DIVERSITY GRADIENTS

Ecologists have long played a leading role in the analysis of diversity, particularly since Hutchinson's (1959) seminal paper. These efforts have been directed primarily toward the solution of two questions: (a) How can latitudinal gradients in diversity be explained? and (b) How can variation in diversity among different habitats be explained? By and large ecologists have considered the answer to the first question to be an extension of the answer to the second. The discussion that follows takes the approach that the answers to the two questions are largely independent—that is, neither is a logical or biological corollary of the other.

Ecological approaches to diversity have been extensively reviewed by others (Connell & Orias, 1964; MacArthur, 1965; Pianka, 1966; Whittaker, 1972, 1977; Ricklefs, 1973; Rosen, 1981; Thiery, 1982), and although each categorizes potential explanations somewhat differently, a common list can be generated.

Explanation 1. The *time-stability hypothesis* states that the longer a community has maintained stability and not been subject to major disturbance (extinction), the more species will accumulate.

Explanation 2. The *spatial heterogeneity hypothesis* predicts more species will co-exist in environments that are more complex spatially. As Pianka (1966: 36–37) noted, the concept of spatial heterogeneity is also a problem of scale, and ecologists, more often than not, refer to local within- or between-habitat complexity when comparing differences in diversity (MacArthur et al., 1962, 1966; MacArthur, 1964; Ricklefs, 1977).

Explanation 3. The *productivity hypothesis* states that as environments increase in productivity, diversity will increase (Connell & Orias, 1964).

Explanation 4. The *competition hypothesis* argues that as competition increases, organisms become more specialized and niche sizes decrease, and hence diversity can increase (MacArthur, 1965, 1972). A variant of this hypothesis states that the evolutionary impetus to reduce competition results in more niche overlap and thus higher species diversity (Klopfer & MacArthur, 1961).

Explanation 5. The *predation hypothesis* states that as predators increase in numbers, they reduce population sizes of their prey, thus allowing more of those species to coexist (Paine, 1966; Janzen, 1970).

Ecologists have been quick to point out that no single hypothesis can explain spatial gradients in diversity, and consequently some combination of the above five explanations is generally invoked (Pianka, 1966; Menge & Sutherland, 1976; Huston, 1979). Yet even this misses the point because supporters of these hypotheses rarely address the question of the rate-control of speciation and extinction (Ricklefs, 1973 is an exception), which, it has been argued, is the first-order cause of large-scale diversity gradients.

Ecological explanations have generally confounded two issues: the generation of diversity versus its maintenance. By and large, ecologists have spoken only to the latter, and thus a causal relationship between their explanations and the underlying determinants of diversity—speciation and extinction—usually is not addressed. Ricklefs' (1973: 714) classification of diversity hypotheses is one attempt to do this, but that effort primarily functions to expose the inconsistencies among some of these hypotheses. For example, competition is said to be more intense in tropical situations, thus increasing natural selection and thereby leading to faster evolution (Dobzhansky, 1950). Yet at the same time, competition is claimed to be *less* stringent in the tropics, thus leading to lower extinction rates (Ricklefs, 1973: 714, table 43-5). Likewise, greater "productivity" is hypothesized to lead to greater turnover of populations, thus increased natural selection, and faster evolutionary (speciation) rates; in contrast, more "resources" also are said to result in less competition, thus damping natural selection and thereby lowering extinction rates.

The hypothesis advanced here is that these presumed ecological correlates of high diversity,

rather than being causes, are simply *effects* of having more species together in the same place. None of them is sufficient to account, in any regular manner, for the spatial gradients of speciation and extinction rates that are necessary to produce observed patterns of diversity. In contrast, these ecological correlates can be explained as consequences of those same gradients. Thus, higher productivity, narrower niches, more niche overlap, more competition, more predation, and more habitat heterogeneity might be expected in communities having relatively more species.

DEEP-SEA DIVERSITY AND TIME-STABILITY HYPOTHESIS

One of the most intriguing spatial gradients of diversity is the increase of the deep-sea benthos relative to the continental shelf and abyssal plain (Hessler & Sanders, 1967; Sanders, 1968; Rex, 1981a, 1981b; see Fig. 4). Although this increase has been explained as an effect of area and thus not requiring a separate deterministic explanation (Abele & Walters, 1979a, 1979b), Rex (1981a) reanalyzed available data and concluded that the additional diversity on the continental slope and rise is not area dependent.

Explanations for the parabolic shape of the deep-sea diversity gradient (Fig. 4) have been ecological, and the time-stability hypothesis has been particularly influential (Grassle & Sanders, 1973; Hessler & Sanders, 1967; Sanders, 1968, 1969). According to this model, the deep-sea environment is much more predictable than that of the continental shelf and supports a "biologically accommodated" fauna. Shelf faunas, on the other hand, are in more stressful environments and are therefore predominately "physically controlled" (Sanders, 1968). Given time, it is hypothesized, these stable environments will accumulate many stenotopic (narrow niched) species whereas shelf environments will be characterized by fewer, more eurytopic species. Original formulations of the hypothesis did not consider the generation of diversity, only its maintenance, but Slobodkin and Sanders (1969) attempted to argue that stenotopic species in the predictable environments would have a higher probability of speciating than would eurytopes in unpredictable situations.

The time-stability hypothesis has not been accepted by some ecologists, particularly because it is difficult to test (Peters, 1976; Abele & Walters, 1979a). Yet alternative explanations have also been ecological and equally difficult to test. Rex (1981a, 1981b) has adopted the "competitive equilibrium" model of Huston (1979) to explain the increased diversity of deep-sea communities. At equilibrium, competition is assumed to eliminate some species, thus lowering diversity. Communities in competitive nonequilibrium, in contrast, are said to maintain higher diversities (curiously, other ecologists have argued that communities in "competitive equilibrium" result in narrower niches and thus more species; e.g., MacArthur, 1965, 1969, 1972). Rex (1981a: 336–338) postulated that the higher diversity of predators on the slope and rise prevents competitive equilibrium, thus raising diversity (see also Rex, 1976).

As Rex (1981a: 338) noted, this hypothesis could account only for the maintenance of diversity, so the problem still remains why there are more species at increased depth, including more predators. Not only does the hypothesis fail to address the question of speciation and extinction rates in a predictive manner, but whether the hypothesis is amenable to empirical evaluation also needs to be considered. How, for example, might one determine whether these deep-sea communities are at equilibrium or not? And, how might the predicted historical roles of competition and predation be evaluated in communities located at depths of 1,500–3,000 meters?

The critical weakness with these ecological hypotheses is that they do not explain gradients in speciation and extinction rates that must exist from the continental shelf to the deep-sea. As discussed earlier, a simpler hypothesis exists: namely, that continental slopes are regions of high geomorphological complexity and that this has promoted a higher rate of speciation. Whether these deep-sea environments have had lower extinction rates than those of the continental shelf or abyssal plain is an open question. Predictability and stability do not imply that an environment will necessarily be more favorable in a physiological sense than are less stable environments, although we might expect greater stability to contribute to lowering the probability of extinction. The time-stability hypothesis, if it has validity or usefulness, would seem to speak only to the issue of a possible difference in extinction rates between environments of the shelf as compared to those of the slope. Present considerations suggest that the deep-sea diversity gradient is better explained by a nonecological

hypothesis that emphasizes variation in speciation and extinction rates.

Conclusions

Conventional interpretations of biological diversification generally are characterized by assumptions that the biosphere is at or near some global equilibrium, that gradients in diversity can be explained by ecological theories of community dynamics, and therefore that speciation and extinction are diversity-dependent. This paper presents an alternative conceptualization of biological diversification and its causes. Some of the main arguments underlying that conceptualization include:

1. The biosphere is a nonequilibrial thermodynamic system, open to a flux of energy and matter from outside the system. The energy-flow from the sun drives biosphere evolution through the transductive capabilities of organisms, namely reproduction and ontogeny. New matter enters the biosphere primarily as a result of the chemical breakdown of the outer surface of the lithosphere.

2. Because the biosphere is an open system, biomass would be expected to increase through time, subject to constraints originating from outside the system. Such constraints would include the physical and chemical properties of the earth and its history.

3. Patterns of diversity are a first-order function of rates of speciation and extinction.

4. The rates of speciation and extinction are diversity-independent. The rate of speciation is hypothesized to be mediated by the rate-change of lithospheric evolution operating through geomorphological complexity. Increased complexity presents more opportunities for vicariance and long-distance dispersal to produce isolation and differentiation.

A deterministic theory of extinction is formulated and relates an increased probability of extinction to an increase in the gradient of environmental harshness. The latter is a measure of the physiological stress to which populations are exposed.

5. The theory of diversification proposed here is testable and has considerable empirical support. Latitudinal and longitudinal gradients of diversity, in both terrestrial and marine environments, can be explained most simply by variation in lithospheric complexity and environmental harshness. The theory, as does any conjecture dealing with complex historical patterns, does not claim to explain all observations; rather, it attempts to account for the greatest amount of variance seen in large-scale diversity gradients.

6. Because the biosphere is an open thermodynamic system, we would not expect the Phanerozoic species diversity curve to show stability, except perhaps over short time periods, and then only because outside constraints (extinction) are damping diversification. Present data support the hypothesis that diversity has not yet reached an upper limit. The exponential rise of the curve itself can be "reset" by mass extinctions or it can be "calibrated" by constraints imposed from outside the system, e.g., by major shifts in global harshness, which might increase the gradient in background extinction.

7. Ecological theories proposed to explain large-scale gradients in diversity have been unsatisfactory because they do not address the first-order causes of these gradients, namely geographic variation in the rates of speciation and extinction. Assumed ecological correlates of high diversity (greater niche specialization and niche overlap, changes in the intensity of competition, increased predation), even if they do exist, are postulated here to be effects of that diversity, not its first-order cause.

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BIOLOGICAL BASIS FOR ADAPTATION IN GRASSES: AN INTRODUCTION

The idea of this symposium, which was held at the 34th Annual AIBS meeting in 1983, began with the question "Why have grasses become one of the most successful plant groups?" The grass family, although only the fourth largest family among flowering plants, is the most dominant and widely distributed. Members of the Poaceae, which account for an estimated 25–45% of the world vegetation, are found in almost every habitat and constitute the dominant species in such biomes as grasslands, steppes, and savannas.

Morphologically, grasses appear to be simple and uniform; their vegetative parts are similar and their flowers consist of little more than stamens and pistil. In the words of Edgar Anderson, they are "stream-lined."

The humble appearance of grasses is, however, deceptive, for these plants have evolved numerous sophisticated modifications in their vegetative and reproductive structures at both macroscopic and microscopic levels. Their adaptive specialization and diversification begin at the level of embryo and seed and proceed through the seedling stage to maturity. Several of these specializations are discussed by the contributors.

Living grass genera and tribes have acquired different combinations of morphological and anatomical characteristics. These grasses could be grouped into several adaptive lines that have radiated from an ancestral complex to exploit specific habitats. The pooid (festucoid) line invaded the temperate region, mostly north of the equator; the arundinoid, a southern, subtropical-temperate region; panicoid, the tropical, humid equatorial zone; andropogonoid, the tropical, seasonal-rainfall zone; chloridoid-eragrostoid, the xeric regions, mostly the dry belts of the tropics of Cancer and Capricorn; bambusoids, temperate and tropical forests; and oryzoids, aquatic habitats. There are numerous other adaptive lines such as the aristidoid, centothecoids, and stipoid, to name a few.

Grasses have also displayed an enormous adaptability to man-made habitats for our most productive crops are the cereals such as wheat, barley, corn, and rice. It is not a coincidence that these cereals became the first staples more than 10,000 years ago. Adaptation to man-made habitats and high fitness in those habitats require special traits such as tolerance to intraspecific competition in monocultural populations.

This enormous and systematic diversity in grasses ought to be based on a rather flexible genetic system that can accommodate changes of different magnitudes. Chromosome number and size are quite variable in grasses and polyploidy is estimated by Professor Stebbins to occur in 80% of the species, with hybridization and apomixis quite common. Some of the odd tribes of grasses such as Lygeeae, Nardeae, Brachyelytreae, and Diarrheneae may have evolved from early, wide hybridization and polyploidy. This genetic system of grasses has been able to accommodate diversification and high efficiency in traits related to fruit dispersal, seedling establishment, wind pollination, interaction and coevolution with grazing regimes, water balance, carbon dioxide and energy exchanges, and others. The next four papers will elaborate on and discuss some of these features and relate them to the success of grasses.

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POLYPLOIDY, HYBRIDIZATION, AND THE INVASION OF NEW HABITATS

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ABSTRACT

Experiments are described showing that most artificial autopolyploids derived from native or introduced perennial grass species from California are far inferior in behavior under field conditions than their diploid ancestors. In a single species, *Ehrharta erecta* in two out of 22 localities, the autotetraploid maintained itself for, respectively, 19 and 39 years, but remained either in the exact locality of planting or in nearby localities having very similar ecological conditions. The control diploids, direct descendants of the progenitors of the autopolyploids, spread more widely and evolved more variation with respect to growth habit among each progeny. These results, along with other evidence derived from several literature sources, strengthen the hypothesis that successful polyploids among natural populations are usually or almost always the result of increased heterozygosity accompanying either interracial or interspecific hybridization. The hypothesis that polyploids succeed because of their greater tolerance of severe ecological or climatic conditions is again rejected, and that which postulates secondary contacts between previously isolated populations as the principal cause for their high frequencies in some groups of angiosperms is favored. The unusually high frequency of polyploids in the Gramineae is attributed to the probable fact that habitats to which they are best adapted have changed in extent and position repeatedly during the geological periods since the initial evolution of the family.

The family Gramineae contains higher percentages of species and races or cytotypes of polyploid origin than any other large family of angiosperms. More than 80% of its species have undergone polyploidy some time during their evolutionary history. Polyploidy is expressed by four different kinds of numerical series, as follows:

(1) Multiples of an original low basic number. Examples: *Triticum, Bromus,* and *Festuca* that include species having somatic numbers of $2n = 14, 28, 42, \ldots$, basic number $x = 7$.

(2) Multiples of a secondary basic number, that was itself derived from the original number by an earlier cycle of polyploidy. Examples: *Poa scabrella* complex, $2n = 42, 84$, $x = 21$ (Hartung, 1946); *Bothriochloa saccharoides* complex, $2n = 60, 120, 180$, $x = 30$ (Gould, 1966); and Australian species of *Danthonia,* $2n = 24, 48, 72$, $x = 12$ (Brock & Brown, 1961).

(3) Multiples of a basic number that is the lowest in its genus, but was probably derived from that of preexisting genera by a cycle of polyploidy in the remote past. Examples: *Oryza,* $2n = 24, 48$, $x = 12$ and *Tripsacum,* $2n = 36, 72$, $x = 18$ (Fedorov, 1969).

(4) Aneuploid series that most probably represent successions of alloploids based upon different basic numbers. Example: *Stipa,* $2n = 22, 24, 28, 32, 34, 36, \ldots 82$. All of the numbers listed in Fedorov (1969) can be derived from various combinations of the basic gametic numbers $x = 5$, 6, and 7.

The existence of these four kinds of situations indicates that polyploids in this family include, in addition to those that have originated recently during the past few thousand years, other polyploids that are intermediate in age from one to several million years and still other genera that acquired a secondary polyploid number during the early evolution of the family 50–70 million years ago. The original basic number for the family has been the subject of much speculation, but no convincing evidence has been presented for any of the various hypotheses. In this writer's opinion, the basic numbers $x = 5$, 6, and 7 are almost equally probable. They could, in fact, have all been acquired by the species complex from which the family first arose. Moreover, the presence of $x = 11$ in *Streptochaeta,* a genus that is very much isolated with respect to morphological characters, and at the same time is a mosaic of very primitive characteristics along with others that are highly specialized, suggests that polyploidy, along with trends toward aneuploidy and a high degree of specialization with respect to some morphological characteristics, evolved quickly and soon after the family first became differentiated. Accordingly, the early stages of grass evolution must have produced many species

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and genera that are now completely extinct. Hence in the absence of diagnostic fossils, any attempt to reconstruct the early evolution of grasses, including the first occurrences of polyploidy must be regarded as futile and self-defeating.

Another distinctive feature of the Gramineae is that the high frequency of polyploidy prevails throughout the family. Nearly all of the other large families of angiosperms: Liliaceae, Orchidaceae, Ranunculaceae, Rosaceae, Leguminosae, Onagraceae, Umbelliferae, Scrophulariaceae, Rubiaceae, and Compositae, include a few large genera in which polyploids are a minority of species or are totally absent. Not so in the Gramineae: its largest genus in which the majority of species are diploids is *Melica,* containing about 60 species; a modest number compared to such giants as *Festuca* (150 spp.), *Panicum* (500 spp.), and *Paspalum* (200 spp.). Because of this situation, Gramineae are not well fitted for making comparisons between related genera that differ greatly from each other with respect to the frequency of polyploidy. Hence in discussing reasons for high frequencies of polyploidy, I shall make comparisons between genera belonging to other families.

Current Hypotheses to Explain High Frequencies of Polyploidy

During the past 60 years, several hypotheses have been advanced to explain different frequencies of polyploidy in a given flora or group of plants. The principal ones are: (1) Many polyploids are more resistant to extreme temperatures, either cold or heat, than their diploid relatives. (2) Polyploids include a higher proportion of drought resistance genotypes than do related diploids. (3) Polyploids are better adapted than their diploid relatives to invasion of new habitats. None of these is entirely satisfactory.

The hypothesis of greater cold resistance, first proposed by Tischler (1935) and more recently supported by Löve and Löve (1949) and others, has been severely criticized by Favarger (1957), Gustafsson (1948), and the present writer (Stebbins, 1950). It is contradicted by most experimental autopolyploids, which are less resistant to frost than are their diploid progenitors. If it were the major reason for high frequencies of polyploidy in Gramineae, we would expect to find higher frequencies of polyploidy in temperate and arctic genera than in tropical genera. As is evident from the high degree of polyploidy in such tropical genera as *Paspalum, Saccharum,* and various genera of Bambuseae, this is not the case. The same criticisms can be raised against the hypothesis that polyploidy has become generally and significantly more prevalent because of present or past exposure to severe drought. With respect to drought, in fact, some examples of increasing polyploidy have been associated with adaptation to more mesic habitats on the part of the higher polyploids. This is true of hexaploid as compared to tetraploid varieties of wheat, tetraploid as compared to ancestral diploid species of perennial Triticeae such as *Elymus* (*Psathyrostachys*) *junceus* (Dewey, 1970), and polyploid as compared to diploid species of *Bouteloua* (Gould, 1966; Stebbins, 1975).

Hence one can safely conclude that greater resistance to cold or drought is not produced by polyploidy or chromosome doubling per se. In some instances, a polyploid cytotype may be more resistant than one of its diploid relatives, but this is probably due to the acquisition of greater resistance from another source, either mutation or, more probably, hybridization.

With respect to both of these hypotheses, a relevant set of data is the geographical and ecological distribution of the 12 species having the highest number of chromosomes known in the family. These are listed in Table 1. They encompass a wide range of taxonomic diversity, including eight tribes (Agrosteae, Andropogoneae, Aveneae, Chlorideae, Danthonieae, Eragrosteae, Festuceae, and Paniceae) and four subfamilies (Arundinoideae, Eragrostoideae, Panicoideae, and Pooideae), thus emphasizing the wide distribution of high polyploidy in the family. Their geographic distribution is equally diverse. They grow in a variety of climatic zones and habitats, from tropical to polar and desert margins, although the largest single category of habitats is cool or warm temperate, and insular, with relatively little seasonal fluctuation in temperature. These data support many others in pointing toward the lack of correlation between distribution of polyploids and any particular kind of habitat or geographic region. The principal reasons for the high frequency of polyploids in grasses must be sought among factors other than edaphic-physiological or geographic.

The only hypothesis that emphasizes other factors is that which postulates greater ability of polyploids to invade and colonize new or disturbed habitats than that of their diploid progenitors. This hypothesis assumes that poly-

TABLE 1. Twelve species of Gramineae having the highest levels of polyploidy.

Species	Somatic Number	Basic Number	Ploidy Level	Geographic Distribution
Alopecurus alpinus	130	7	18–20*x*	Circumpolar
Andropogon (*Bothriochloa*) *barbinodis*	180	10	18*x*	SW United States, Mexico
Calamagrostis crassiglumis	140	7	20*x*	Pacific North America
Ctenium concinnum	160	10	16*x*	South Africa
Danthonia induta	120	6	20*x*	Southwestern Australia
Dupontia Fisheri	132	11	12*x*	Arctic
Echinochloa stagnina	126	9	14*x*	Assam, India
Helictotrichon (*Avena*) *pratense*	126	7	18*x*	Britain, Scandinavia
Poa litorosa	263–265	7	38*x*	Auckland Islands, New Zealand
Poa rigens	127	7	18*x*	Iceland
Saccharum robustum	194	10	18–20*x*	New Guinea
Sporobolus airoides	126	9	14*x*	SW United States

ploids can arise and maintain themselves in a variety of habitats, depending upon their genetic constitution, but only those having an unusually strong capacity for colonization will become widespread. It was advanced by Reese (1958) as an alternative explanation for the high frequency of polyploids in the flora of northern Europe and has been supported by the present author (Stebbins, 1972), Darlington (1973), and Ehrendorfer (1980). It is, however, incomplete. It simply raises another question: How do successful, widespread polyploids acquire their greater capacity for colonization? The following sections of this contribution will be devoted to a discussion of this problem.

ARTIFICIAL TETRAPLOID *EHRHARTA ERECTA*: A LONG TERM FIELD EXPERIMENT

The most direct evidence that can be obtained on the possible effect of polyploidy in increasing evolutionary success consists of field experiments in which polyploids and their known diploid ancestors are planted simultaneously in the same area and their relative success is compared. With respect to strict autopolyploids of non-hybrid origin, the one that I have conducted during 39 years on a South African species, *Ehrharta erecta*, which became established as an adventive in northern California about 1930, is the most extensive and long lasting that is known to me. As stated in the account published with the record of the first few years of this experiment (Stebbins, 1949), it was begun after screening colchicine induced polyploids belonging to 20 species and nine genera of grasses, the diploid progenitors of which all are well adapted to persistence in the natural vegetation of northern California. Of these species, only *E. erecta* survived the preliminary screening and was judged worthy of comparing the artificially induced autopolyploid with its diploid progenitor under a variety of conditions. Autopolyploids derived from all of the other species failed completely. Consequently, the results of this experiment can be interpreted as indicating the maximum success that the non-hybrid autopolyploid of a grass species can achieve in a semi-natural habitat in comparison with its diploid progenitor.

The fact should be emphasized that the experiment to be reviewed below was not a single, isolated effort. It was, rather, the most successful of a series of attempts to establish in nature artificially induced tetraploids belonging to several different and diverse genera.

In all, 22 different plantings were made of diploid and autotetraploid *Ehrharta*, some of which consisted of seed sown in plots 5 × 5 m^2, the diploid plot being sown adjacent to that of the tetraploid, while others were started by planting well-rooted clonal divisions, in which diploids and tetraploids alternated with each other. As shown previously (Stebbins, 1949), distinctive morphological characters enabled me to follow the spread or extinction of diploids and tetraploids, but from time to time these results were checked by actual chromosomal counts. Sixteen of the plots were on the campus of the University of California, Berkeley, and two each in the inner Coast Ranges of Napa County, the campus of

FIGURE 1. Three plants of *Ehrharta erecta*, descendants of the planting made in 1943, dug in 1972 in the neighborhood of Plot 7, Strawberry Canyon, Berkeley and growing under uniform conditions in a greenhouse, 1973. At left a plant from the original diploid planting; center, a plant from about 30 m up the hill, in beaten ground under a picnic table; at right, a plant from about 100 m away, in deep shade of a planted redwood grove. All of these plants are diploid; variation of this kind was not observed among the tetraploids.

the University of California at Santa Cruz, and the town of Carmel, Monterey County.

Although diploid *E. erecta* has survived and is reseeding itself in most of the plots, and from some of them has spread extensively into surrounding areas, the autotetraploid has failed completely except in two of them, both of them in Strawberry Canyon near Berkeley's Botanical Garden. The one described as Plot 7 in the previous account (Stebbins, 1949) has been followed for 39 years. Up until 1948, the tetraploid was more successful there than was the diploid. A few years later a small building was erected just below this plot, and apparently dirt from the excavation that contained seeds of *Ehrharta* was thrown into a grove of oaks where no planting had been made. This condition was first noticed in 1957, and the frequency of diploids and tetraploids was determined in the accidentally seeded lower area in 1965. In the area as a whole, the number of established plants was: diploids 200, tetraploids 230. The distribution patterns of the two cytotypes was highly distinctive: as in the originally seeded upper plot, the tetraploid plants were concentrated in that portion of the area that occupied the steepest, best drained slope, and was most heavily shaded under *Quercus agrifolia*. For several years after these observations were made, little change was noticed, but about 1965 *Ehrharta* spread extensively westward. The plants colonized relatively diverse areas, some of them in hard packed soil and others in well-drained areas under redwoods (*Sequoia sempervirens*). In 1972 these areas were plotted and the most extreme types, including some that resembled the original tetraploids, were taken to the greenhouse for chromosome counting. All of them proved to be diploids. Nevertheless, some of them maintained their characteristic growth habits under uniform conditions, as shown in Figure 1.

The first plot planted in 1943 and the second pair of plots established in 1964 show similar results. In both areas, the diploid has spread ex-

tensively and the autotetraploid, although it still maintains itself, has remained in the type of habitat that exists where it was first established, and has decreased in numbers.

The relative lack of success of tetraploid *E. erecta* during the long period of the principal experiment cannot be ascribed to low seed fertility. Although precise records of seed fertility have not been kept, it has consistently been higher than 80%, and during the first years of the experiment, large numbers of seedlings were found every year near the mother plants.

These experiments should not be interpreted to mean that autopolyploids are always inferior to allopolyploids as colonizers of new habitats. Those that are derived from hybridization between genetically compatible ecotypes of the same species, or between genetically different diploid genotypes that exhibit good combining ability may often be superior to their parents. This conclusion is supported by the experience of agronomists who have attempted to breed new autotetraploids of commercial value. The most extensive efforts in this direction have been made by Müntzing (1954) with cereal rye. He has achieved success only by intercrossing cultivars either at the original diploid level or their induced tetraploids, in order to increase the base of genetic diversity. Dealing chiefly with alfalfa (*Medicago sativa*), Bingham (1980) has emphasized further the importance of hybridization and heterozygosity for the production of successful autopolyploids. How does this relate to the situation in nature?

POLYPLOIDY AMONG SPECIES THAT HAVE RECENTLY COLONIZED NEW AREAS

Except for intentional attempts at introduction, like that just described for *Ehrharta,* the most direct evidence available that bears on the problem can be obtained by comparing chromosome numbers of the same species or closely related species pairs, some populations of which are in their original native habitat, while others have been introduced in historical times into a new region. Recent spontaneous allopolyploidy is known for two such examples: *Spartina townsendii* (*S. maritima* × *alterniflora*) (Marchant, 1966) and *Tragopogon mirus* plus *T. miscellus* (Ownbey, 1950). These examples show that new allopolyploids can often be highly successful. On the other hand, a large number of diploid species have become adventive and established in large populations as adventives on continents different from their original homes. In many of them, diploid chromosome numbers have been counted both in their original home and on the continent where they are adventive. Fingering through the chromosomal encyclopedia edited by Fedorov (1969), I find 14 such examples in the Gramineae (Poaceae) alone. Admittedly, this evidence is weak. If autopolyploids of adventive species, originating recently, had still a much restricted geographic distribution they could easily be overlooked. Nevertheless, in some genera, such as *Tragopogon,* in which even the diploids have very large achenes, the increase in size that would certainly accompany autopolyploidy would be likely to receive attention. A reasonably safe statement is that in *Tragopogon* species established as adventives in the New World, allopolyploidy has been a more successful evolutionary change than autopolyploidy.

Another kind of indirect evidence is derived from comparing the frequency of polyploidy in neighboring genera of the same family, or in different subgenera of the same genus. If the source of polyploid series is autopolyploidy in which the change in chromosome number is the chief reason for success, no difference would be expected between these closely related groups, particularly if they have similar geographic and ecological distributions. On the other hand, if a major reason for success depends upon generating and maintaining favorable new gene combinations following hybridization between previously separated populations in areas of secondary contact, then the frequency and success of polyploids in a genus or subgenus should be positively correlated with the number of secondary contacts that have been made during its evolutionary history. This number would obviously be greater for groups that, because of their ecological preferences, tend to have a "patchy" distribution than for those that contain species that are distributed chiefly in more continuous habitats such as climax forests and riverine habitats.

Two families that exhibit, in a dramatic fashion, the pattern predicted on the basis of the secondary contact hypothesis are the Salicaceae and Betulaceae. In the Salicaceae, species of *Populus* are mostly confined to the margins of streams and rivers, and so exhibit continuous distribution patterns. All of the established species are diploid, although individual polyploid trees are not uncommon. On the other hand, the species of *Salix* include both riverine species and those

that have patchy distributions in early stages of forest succession or on mountain slopes. Among them are many polyploids, having chromosome numbers as high as $2n = 190$ (Fedorov, 1969). In the Betulaceae, the genera *Carpinus, Corylus,* and *Ostrya* grow in well-developed continuous forests, often on stream margins. All but one are diploid. Species of *Betula* grow in a variety of habitats, but many of them are found principally on mountain slopes and in bogs, and therefore patchy distribution patterns were likely to have been found also in the past. Of the 37 species of *Betula* that have been counted, 19 are polyploid or contain polyploid cytotypes, their polyploidy being well correlated with ecological preferences that would favor patchy distribution patterns.

Another family that provides evidence of this kind is the Liliaceae. Among forest loving genera like *Lilium, Disporum,* and *Trillium,* polyploid series are rare. Related genera, having species adapted to more open, patchy habitats like *Tulipa, Gagea,* and *Lloydia* contain high percentages of polyploid species and cytotypes.

Among the Gramineae, differences of this kind are rare, since nearly all of the larger genera contain high percentages of polyploids. Nevertheless, suggestive patterns exist in the subfamily Bambusoideae, that have been carefully analyzed by Soderstrom and his associates (Soderstrom, 1981; Hunziker et al., 1982). Bamboos are of particular importance in this connection, since they are confined to mesic forests or forest margins, almost entirely in the tropics, and never in climates or situations characterized by extremes of drought or cold. Soderstrom divides the subfamily into two groups: the woody bamboos, containing chiefly the tribe Bambuseae; and the herbaceous bamboos, that resemble typical bamboos in most of their reproductive characteristics but are low growing, herbaceous, and confined to the understory of tropical rain forests. They include several tribes. Assuming that basic gametic numbers are $x = 12$, 11, and 10 (the probable polyploid origin of these numbers is discussed later in this article), the 108 woody species that have been counted include 86 tetraploids and 18 hexaploids making 96% polyploidy, while the 35 herbaceous species include six tetraploids, or 17%. A further point of great importance is that within the woody group the same level of polyploidy exists within entire genera or groups of genera, while two of the herbaceous genera include both diploids and tetraploids.

These differences are best explained by assuming that the polyploidy among the woody group is more ancient than among the herbaceous group, in agreement with conclusions about woody angiosperms in general, as compared to herbaceous groups (Stebbins, 1980; Ehrendorfer, 1980; Raven, 1975). The hypothesis is that arboreal bamboos first became differentiated in forest margins, perhaps in montane regions, where patchy distributions and frequent secondary contact promoted the success of hybrid polyploids. These became the ancestors of modern genera and tribes. More recently, successful species of woody bamboos have become incorporated into forest floras, have reduced tendencies for colonization and secondary contact, and so do not exhibit polyploid series. Herbaceous bamboos, on the other hand, have always been adapted principally to the understory of rain forests, but from time to time have become colonizers in connection with which they have given rise to a few polyploid species within genera that still contain diploids.

The implications of this hypothesis are far-reaching. First, the success of polyploid cytotypes, species, and genera is connected only indirectly to increase in chromosome number per se and is due primarily to favorable gene combinations that they contain. As I have repeatedly emphasized elsewhere (Stebbins, 1950, 1980), polyploidy throughout the continuous spectrum that extends from auto- to allopolyploidy buffers and tends to preserve favorable gene combinations, particularly those in which adaptive fitness depends largely upon heterozygosity and epistatic gene interactions. Buffering is achieved in two different ways: tetrasomic inheritance ratios and preferential pairing of completely homologous chromosomes, i.e., those having identical or very similar nucleotide sequences in their DNA. These mechanisms have been described in numerous publications, including those that have been cited, and need not be repeated here.

The secondary contact hypothesis predicts that isolated polyploid races as well as localized autopolyploid cytotypes should be found in many diploid or homoploid species: this prediction is in accord with presently available data. On the other hand, the difference between failure, localized establishment, and widespread success depends not upon changes in chromosome number but upon acquisition of favorable gene combinations. Although these may sometimes arise by mutation alone, they are much more likely to arise among the diverse segregants that arise after

hybridization between previously isolated and adaptively differentiated populations. These populations may be interfertile races of the same species so that polyploid segregants from their hybrid would be autopolyploids. Other diploid ancestors may belong to distinct species that form sterile hybrids at the diploid level so that polyploid derivatives would incorporate various degrees of allopolyploidy. Again, what counts is the adaptiveness of population environment interactions, not the taxonomic status of parental populations.

CYCLES OF POLYPLOIDY IN THE GRAMINEAE

As stated in the introduction, one reason for unusually high levels of polyploidy in Gramineae is the frequent establishment of polyploid basic numbers after an initial cycle of polyploidy followed by diploidization. This condition is best interpreted by assuming that within the same genus occur successive cycles of polyploidy, between which evolution takes place at homoploid levels. The secondary contact hypothesis would predict that these cycles would coincide with periods when maximal probabilities existed for separation, differentiation and later reunion of populations. Does the evolution of the family as we know it agree with such a prediction?

Unfortunately, the fossil record is too incomplete to provide a definite answer to this question. Nevertheless, shifts in paleoclimates, particularly at the end of the Cretaceous and throughout the Tertiary Period, lend support to this assumption. In agreement with most modern discussions of the phylogeny of the family, I assume that the earliest grasses inhabited margins of tropical forests, then invaded open tropical savannas, entered still later into expanding temperate grasslands during the middle and end of the Tertiary Period, and finally occupied weedy habitats created by human disturbance after the retreat of the Pleistocene glaciers.

The first cycle of polyploidy occurred probably soon after the family originated in the Upper Cretaceous Period. From the widespread initial base numbers of $x = 6$ and 5 arose in different groups the secondary base numbers $x = 12$ and 11. The following facts support retention of the hypothesis that the base numbers $x = 10$, 11, and 12 are not primitive as suggested by Raven (1975), but derived by polyploidy from $x = 5$ and 6. First, they appear in a few distantly related groups that are among the most primitive genera of their tribes, such as *Danthonia* and *Pentaschistis* in the Danthonieae, as well as *Elionurus* (Kammacher et al., 1973) and *Sorghum* in the Andropogoneae. Second, the alternative hypothesis proposed by Raven that $x = 7$, 6, and 5 are derived by aneuploid reduction from $x = 12$ is made improbable by the extreme rarity of $x = 8$ in the family as a whole, and the almost equal rarity of $x = 9$ except in highly specialized members of the Paniceae and Erogrosteae. The early cycles of polyploidy may well have been associated with mountain building "revolutions" that took place at the end of the Cretaceous Period and brought about many shifts in the location of forests and forest margins. The second cycle may have coincided with the opening up of warm savanna habitats during the Eocene epoch, particularly in South America, where the first grazing mammals evolved (Andreis, 1972; Patterson & Pascual, 1968). Fragments of siliceous bodies found in Eocene loess deposits of South America are most probably remnants of Eocene grasses (Frenguelli, 1930). Entrance into north temperate habitats is documented partly by the numerous fossil grass seeds that have been found on the plains of North America (Stebbins, 1950; Thomasson, 1978) and may well have coincided with shifts in position, expansion, and contraction of temperate grasslands. These events were followed by extensive mountain building throughout the world during the Pliocene epoch creating, in the Northern Hemisphere, the continental type of climate characterized by great seasonal differences in temperature to which the majority of genera belonging to the tribe Festuceae are adapted. New polyploids probably arose more or less continuously during the Pliocene and Pleistocene epochs, their evolution being stimulated by the advances and retreats of the Pleistocene glaciers and the shifts in vegetation that accompanied them. A final cycle of polyploidy, affecting chiefly weedy genera like *Bromus*, *Triticum* (*Aegilops*), *Hordeum*, *Eragrostis*, *Chloris*, and *Digitaria*, took place in association with human disturbance and cultivation since the retreat of the glaciers and the onset of warmer climates through much of the world. In my opinion, Gramineae contain higher percentages of polyploids, both primary and secondary, than do other families of angiosperms because their favored habitats and methods of reproduction preadapted them particularly well for taking advantage of the climatic cycles just outlined.

Summary and Conclusions

The percentage of species having had polyploid events during their evolutionary history is in the Gramineae between 80 and 90%, the highest of any large angiosperm family. This includes both polyploid series within genera and ancient polyploidy that gave rise to high basic diploidized numbers for many genera. The evidence presented indicates that this high percentage exists not because the grass genome is more prone than others to the occurrence of polyploid individuals within populations or that raw autopolyploids are in any way superior to their diploid progenitors, but because frequent opportunities for secondary contact and hybridization between differentiated diploid populations have generated highly adapted, aggressive gene combinations that have been buffered and maintained largely by the effects of polyploidy in favoring tetrasomic inheritance and preferential pairing of homologous, as compared to partly homologous (homeologous), chromosomes.

1. Comparison between artificially produced autopolyploids and their diploid ancestors, particularly an experiment of 39 years' duration with *Ehrharta erecta,* has shown that without hybridization, autopolyploids, even when highly fertile, are greatly inferior to their diploid progenitors under field conditions or at best can maintain themselves but lack aggressiveness and the ability to invade new habitats.

2. The hypotheses advanced by early workers that polyploids owe their success to their greater ability to withstand severe ecological conditions, such as cold and drought, have been refuted by recent data showing that polyploids are nearly or quite as successful under favorable mesic tropical conditions as in arid and cold regions.

3. Comparing genera in various families, some having high and others low frequencies of polyploidy, a correlation is found between high frequencies of polyploidy and patchy geographical or ecological distributions, which have permitted many secondary contacts between differentiated populations.

The secondary contact hypothesis just proposed is supported also by the fact that throughout the geological periods during which the family Gramineae has evolved, habitats favored by grasses such as forest margins, savannas, temperate grasslands, and arctic-alpine tundra have become alternately extended and localized and have changed their geographic positions. These successive habitat changes have promoted the successive cycles of polyploidy that are needed to explain both the high frequency and the high levels of polyploidy found in the family.

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ADAPTATION OF GRASSES TO WATER STRESS—LEAF ROLLING AND STOMATE DISTRIBUTION[1]

R. E. REDMANN[2]

ABSTRACT

Leaf dimension, degree of leaf rolling or folding, and stomatal densities on adaxial and abaxial leaf surfaces were measured on herbarium specimens of 39 grass species from a range of dry to wet habitats in western Canada. Stomata were counted on vinyl leaf impressions taken from the herbarium specimens. Representative surfaces also were examined using scanning electron microscopy. All species from dry habitats had narrow rolled or folded leaves (4 mm or less). The proportion of stomata on the abaxial surface of species from dry habitats ranged from 0 to 65%, but 56% of the species were strongly amphistomatous. The results were compatible with a conceptual model predicting that rolling, amphistomatous leaves would be selected for habitats in which water supply and demand fluctuate widely on seasonal or diurnal time scales.

The evolutionary adaptation of grasses involves a syndrome of physiological, anatomical, and morphological characteristics. Grass leaf structure is closely coupled with major physiological processes such as photosynthesis, water relations, and energy balance. For example, vascular bundle and mesophyll cell arrangement are related to the type of photosynthetic pathway (Black et al., 1973; Hattersley & Watson, 1975), which, in turn, can influence niche separation in grasses (Monson et al., 1983). Specialized leaf tissue structure in some grasses results in leaf rolling, which strongly influences water and energy balances by changing the characteristic leaf dimension and the conductance of heat, water vapor, and carbon dioxide (Ripley & Redmann, 1976). This paper concentrates on the relationship between leaf rolling and stomatal distribution and conductance.

The anatomy and mechanism of leaf rolling in grasses have been studied for over a century (Tschirch, 1882; Shields, 1951). Loss of turgor in the bulliform cells on the adaxial (upper) surface generally is considered to induce rolling. Shrinkage of the adaxial subepidermal sclerenchyma and mesophyll, due to water loss, also contributes to involution; rolling can occur in leaves that lack bulliform cells (Shields, 1951). Some grasses have permanently rolled or folded leaves.

Leaves of native grasses from semi-arid grassland roll in response to increased plant water stress during dry periods (Ripley & Redmann, 1976). More mesic grasses such as cereal crops also exhibit leaf rolling when exposed to water stress (Hurd, 1976; O'Toole et al., 1979). Leaves of *Sorghum bicolor* roll and unroll in response to diurnal changes in plant water status, provided stress is not too severe (Begg, 1980).

The early textbooks on plant ecology generally explained rolling as a xeromorphic adaptation for reducing transpiration by "protecting" the stomata, which were considered to be concentrated on the upper surface (Warming, 1909; Weaver & Clements, 1929; McDougall, 1949). Unfortunately, references to data supporting this explanation were not given, but the idea probably originated with early work on ecological plant anatomy. Tschirch (1882) classified grasses as meadow type, with flat leaves, or steppe type, with rolling leaves. Lewton-Brain (1904) grouped British grasses into four categories representing progressively more drought resistant types: (1) leaves with flat upper surfaces, amphistomatous, (2) leaves with ribbed upper surfaces, amphistomatous, (3) leaves with ridged upper surfaces, rolled with drying, epistomatous, and (4) leaves permanently rolled or folded, epistomatous.

I was unable to find published comparative data on relative stomatal distributions on grass leaves in relation to rolling or drought resistance that would verify the generalizations described above. Parkhurst (1978) pointed out that the limited data in the literature show no clear trends

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TABLE 1. Leaf characteristics of grasses from a range of habitats. All collections from Saskatchewan unless noted otherwise.

Species	Leaf Shape[a]	Stomata ad/ab %	Leaf Type[c]	Measured Leaf Width (mm)[b]	Drought Resistance Index	Habitat
Festuceae						
Bromus ciliatus L.	fl	95/5	Fe	10	7	Boreal forest
B. pumpellianus Scribn.	fl	40/60	Fa	5	6	Boreal forest opening
Festuca saximontana Rydb.	fo	100/0	PRe	1.5 (0.5)	1	Sandy grassland
F. scabrella Torr.	fo	100/0	PRe	3 (1)	4	Mesic grassland
Poa arida Vasey	fl–fo	70/30	Ra	2.5	1	Sandy grassland
P. palustris L.	fl	60/40	Fa	6.5	8	Floodplain forest
P. secunda Presl.	fl–fo	70/30	Ra	1.5	1	Xeric grassland
Scholochloa festucacea (Willd.) Link	fl–i	60/40	Ra	7	10	Prairie wetland
Aveneae						
Alopecurus aequalis Sobol.	fl	50/50	Fa	5	9	Boreal wetland
Beckmannia syzigachne (Stued.) Fernald	fl	50/50	Fa	8	9	Prairie wetland
Calamagrostis canadensis (Michx.) Beauv.	fl	100/0	Fe	5	8	Boreal forest
C. montanensis Scribn.	fl–i	60/40	Ra	3	1	Xeric grassland (Alberta)
Cinna latifolia (Trevir.) Griseb.	fl	50/50	Fa	9	7	Boreal forest
Helictotrichon hookeri (Scribn.) Henr.	fl–fo	85/15	Re	4	4	Mesic grassland
Hierochloe odorata (L.) Beauv.	fl–i	70/30	Ra	5	8	Boreal wetland
Koeleria cristata (L.) Pers.	fl–i	60/40	Ra	2	2	Clayey grassland
Phalaris arundinacea L.	fl	55/45	Fa	14	10	Prairie wetland
Triticeae						
Agropyron dasystachyum (Hook.) Scribn.	fl–i	65/35	Ra	3	3	Clayey grassland
A. smithii Rydb.	fl–i	50/50	Ra	4	2	Clayey grassland
A. spicatum (Pursh) Scribn. & Smith	fl–i	65/35	Ra	3	2	Sagebrush (Wyoming)

TABLE 1. Continued.

Species	Leaf Shape[a]	Stomata ad/ab %	Leaf Type[c]	Measured Leaf Width (mm)[b]	Drought Resistance Index	Habitat
A. subsecundum (Link) Hitchc.	fl	60/40	Fa	7	6	Boreal forest opening
A. trachycaulum (Link) Malte.	fl	75/25	Fa	7	6	Boreal forest
Elymus canadensis L.	fl–i	70/30	Ra	8	6	Sandy river bank
E. cinereus Scribn. & Merr.	fl–i	55/45	Ra	15	6	Cultivated plots
E. innovatus Beal.	fl	80/20	Fe	6	6	Boreal forest
E. virginicus L.	fl	90/10	Fe	7	7	Deciduous forest
Meliceae						
Catabrosa aquatica (L.) Beauv.	fl	40/60	Fa	8	9	Streamside
Glyceria grandis S. Wats.	fl	60/40	Fa	7.5	9	Streamside
G. striata (Lam.) Hitchc.	fl	70/30	Fa	5.5	9	Streamside
Schizachne purpurascens (Torr.) Swallen	fl–fo	95/5	Re	4	5	Boreal forest opening (Alberta)
Stipeae						
Oryzopsis asperifolia Michx.	fl–i	90/10	Re	7	7	Boreal forest
O. hymenoides (Roem. & Shult.) Ricker	i–fl	35/65	PRa	3 (1)	3	Sandy grassland
O. pungens (Torr.) Hitchc.	fl–i	100/0	Re	2	3	Boreal forest opening
Stipa comata Trin. & Rupr.	fl–i	85/15	Re	3.5	1	Xeric grassland
S. curtiseta (A. S. Hitchc.) Barkworth	fl–i	95/5	Re	2.5	3	Boreal forest opening
S. richardsonii Link	i	100/0	PRe	2 (1)	5	Boreal forest opening
S. spartea Trin.	fl–i	60/40	Ra	2.5	5	Mesic grassland
S. viridula Trin.	fl–i	75/25	Ra	3	4	Mesic grassland
Arundineae						
Phragmites communis Trin.	fl	45/55	Fa	25	10	Boreal wetland

[a] fl = flat, fo = folded, i = involute or convolute.

[b] Folded or involuted width is given parenthetically only for permanently rolled or folded leaves.

[c] Fa = flat, amphistomatous; Fe = flat, epistomatous; Ra = rolling or folding amphistomatous; Re = rolling or folding, epistomatous; PRa = permanently rolled or folded, amphistomatous; PRe = permanently rolled or folded, epistomatous.

regarding the relationship of drought resistance to adaxial-abaxial stomatal distributions. Parkhurst concluded from a survey of four families that amphistomatous leaves occur most often in xeric and hydric habitats; however, he did not include grasses in his analysis.

Absolute stomatal density varies widely among species and with environmental preconditioning (Muenscher, 1915; Salisbury, 1927). The relative numbers of stomata on upper and lower surfaces are not as strongly influenced by preconditioning. Salisbury (1927) found that stomatal density on upper and lower surfaces tends to "augment or diminish in a parallel manner" depending on growth conditions. Tan and Dunn (1975) showed highly significant positive correlations between adaxial and abaxial surfaces of *Bromus inermis* for both stomatal frequency and length.

Pospisilova and Solarova (1980) concluded that the ratio of adaxial and abaxial conductances was only "crudely" related to the ratio of stomatal densities on the two surfaces. However, the proportion of carbon dioxide exchange through the adaxial and abaxial surfaces of *Zea mays* is related to the relative number of stomata on each surface (Bertsch & Domes, 1969). For purposes of the conductance model described later in this paper it is sufficient that the ratio of stomata on each leaf surface indicates at least the trend in the proportion of total conductance contributed by each surface.

The first objective of the work reported here was to determine the relationships between degree of leaf rolling, leaf dimension, and stomatal distribution for grass species collected from native habitats with different water stress regimes. The second objective was to develop a conceptual model to help explain the advantages of different stomatal distribution patterns and leaf rolling in wet or dry habitats.

METHODS

The grass flora of the Prairie Provinces of western Canada was surveyed in order to select species from a range of habitat types along a gradient of water availability. The species were assigned a drought resistance index (DRI) value based on information from descriptions in Best et al. (1971) and Hitchcock (1950), in addition to discussions with V. L. Harms, a taxonomist with extensive experience collecting in western Canada. The DRI ranged from 1 (species present in the driest habitat) to 10 (species present in the wettest habitat). Specimens from the W. P. Fraser Herbarium, University of Saskatchewan, were selected for measurements of leaf width, degree of rolling or folding, and stomatal density on adaxial and abaxial surfaces. In a few cases the DRI was modified slightly depending on annotation data for the particular specimen selected.

Stomatal density was determined on fully-developed leaves from mid-culm position, or on basal leaves, where culm-leaves were small or absent. In all cases impressions were made at the mid-blade position of the adaxial and abaxial surfaces in order to standardize the sampling. Impressions were made using 0.3 mm thick transparent polyvinyl chloride film. Details of the method are described in Redmann (1985). This technique was successful even with leaves having trichomes and corrugated adaxial surfaces.

The number of stomata in a minimum of ten fields randomly located on the impression was determined at 500× magnification. In a few cases where stomatal density was small, counts were made at 125×. The mean stomatal density per mm^2 for each surface was used to calculate percentages of total number of stomata on adaxial and abaxial surfaces. Variation in percentages of the total number of stomata on the two surfaces of leaves from five plants in a population of *Phalaris arundinacea* was smaller than variation in absolute stomatal density. This was because densities on the surfaces increased or decreased together, as was found by Salisbury (1927) and Tan and Dunn (1975). Only percentage ratios are presented here in order to avoid some of the difficulty in comparing species with widely-differing absolute stomatal densities. Because only one or two populations of each species were sampled, variability among different populations of each species was not assessed. Even relatively large variation in percentage ratios (e.g., 15–20%) probably would have little effect on the conclusions reached.

Maximum flattened leaf width was determined on each herbarium specimen. The degree of rolling or folding on the dried specimens was noted and used to supplement information on folding, involution, or convolution reported in Best et al. (1971) and Hitchcock (1950). Leaf surfaces of eight species with widely different DRI values were examined using a Philips 505 scanning electron microscope. Micrographs for three species with distinctive surface features were selected for inclusion here.

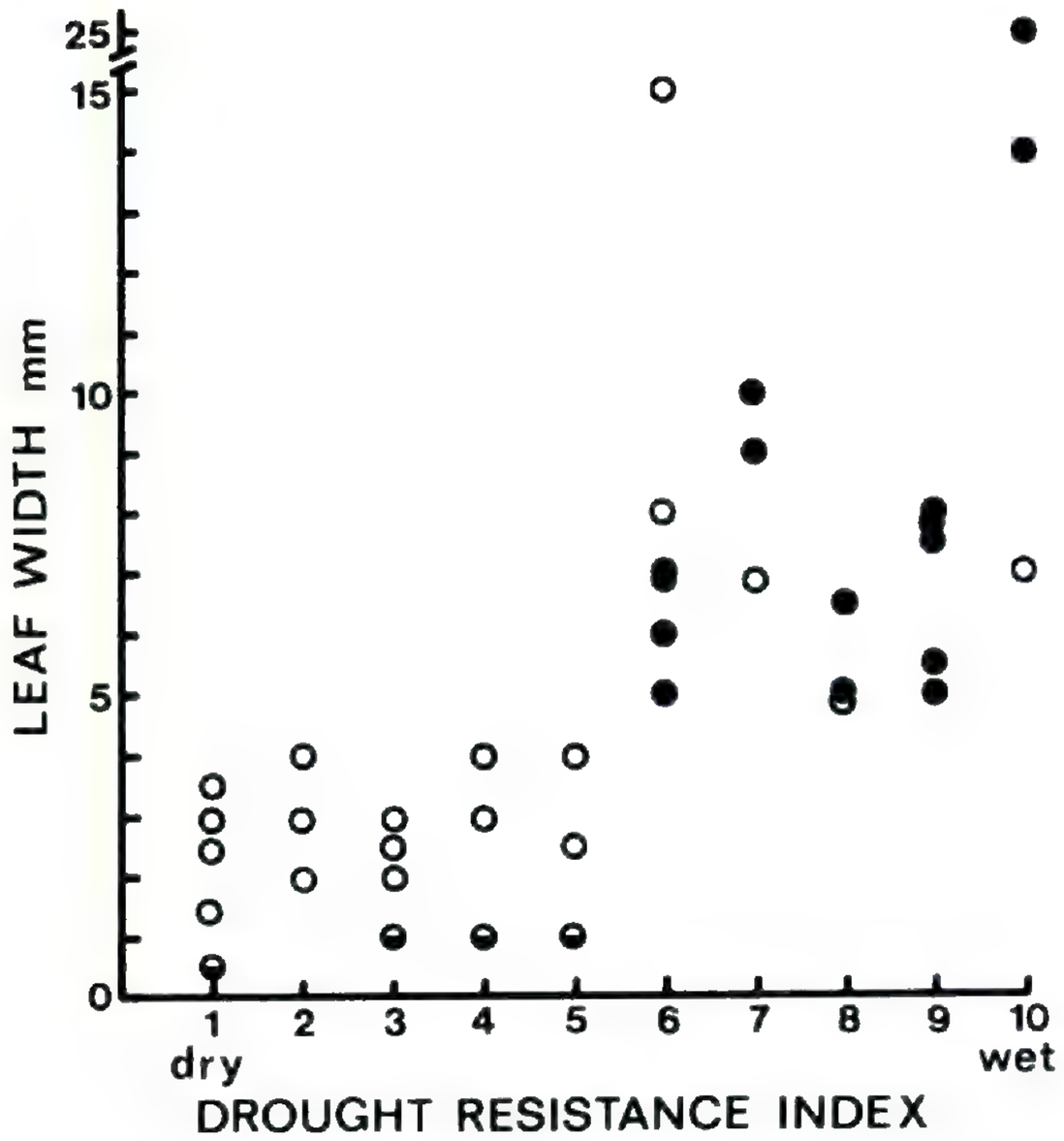

FIGURE 1. Relationship between measured leaf width and drought resistance index for 39 grass species from Saskatchewan and adjacent areas. Closed circles represent flat leaves, open circles are rolling or folding leaves, and half-closed circles are permanently rolled or folded leaves.

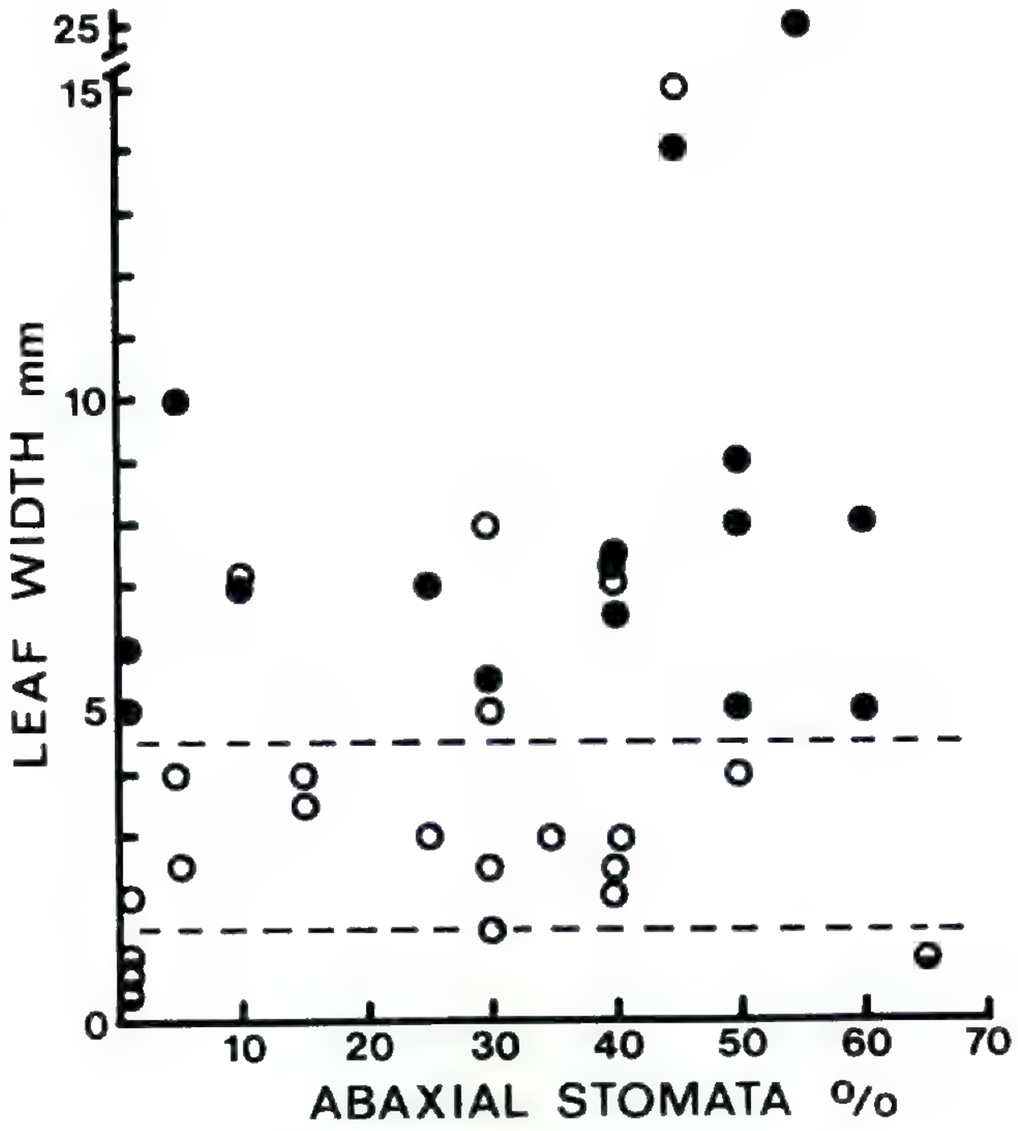

FIGURE 2. Relationship between leaf width and percentage of stomata on the abaxial surface for 39 grass species from Saskatchewan and adjacent areas. Closed circles represent flat leaves, open circles are rolling or folding leaves, and half-closed circles are permanently rolled or folded leaves. Upper dashed line at 4.5 mm is the approximate border between dry-site species and wet-site species. Lower dashed line is the approximate-border between permanently rolled or folded leaves and other types.

RESULTS

The 39 grass species included in Table 1 occur in a range of habitats in western Canada and adjacent geographic regions. The four major tribes (Gould, 1968), Festuceae, Aveneae, Triticeae, and Stipeae each have representatives from several habitat types. The minor tribes, Meliceae and Arundineae, include mainly wetland types. Tribes with the C4 photosynthetic pathway (Waller & Lewis, 1979) were excluded because their special physiology and higher water use efficiency might have complicated the analysis.

In the populations sampled, 19 species have flat leaves that either roll or fold on drying. *Festuca saximontana, F. scabrella, Oryzopsis hymenoides,* and *Stipa richardsonii* have leaves that are more or less permanently folded or rolled. The remaining 16 species have flat, non-rolling leaves.

Leaf widths ranged from 1.5 mm in *F. saximontana* and *Poa secunda* to 25 mm in *Phragmites communis*. There was a clear relationship between drought resistance index (DRI) and leaf width (Fig. 1). No species with a DRI of 5 or lower had a maximum leaf width greater than 4 mm. All four species with more or less permanently rolled or folded leaves had diameters or widths of 1 mm or less. None of the species with a DRI of 6–10 had a leaf width less than 5 mm.

Neither leaf width nor stomatal distribution showed a clear relationship to tribe (Table 1). In the Stipeae, five of the eight species had stomata mainly on the adaxial surface; the exceptions were *O. hymenoides, Stipa spartea,* and *S. viridula.* The average adaxial/abaxial stomatal ratio for each tribe was: Stipeae 80/20, Festuceae 74/26, Triticeae 68/32, and Aveneae 64/36.

There was no correlation of stomatal density on leaf surfaces with either DRI or leaf width (Fig. 2). The results do show that all species with leaves less than about 4.5 mm wide either had flat leaves that rolled or folded, or had permanently rolled or folded leaves. However, the proportion of stomata on the abaxial surfaces of these leaves varied from 0 to 65%. Ten of 18 species (56%) classified as DRI 1–5 had at least 25% of their stomates on the abaxial leaf surface. Six of 21 species with a DRI of 6–10 had 25% or fewer stomata on the abaxial surface. The mean percentage of abaxial stomata (and coefficient of variation, c.v.) for the 18 species with DRI 1–5 was 23.9% (c.v. = 83%), and for the 21 species with DRI 6–10 was 35% (c.v. = 51%). These

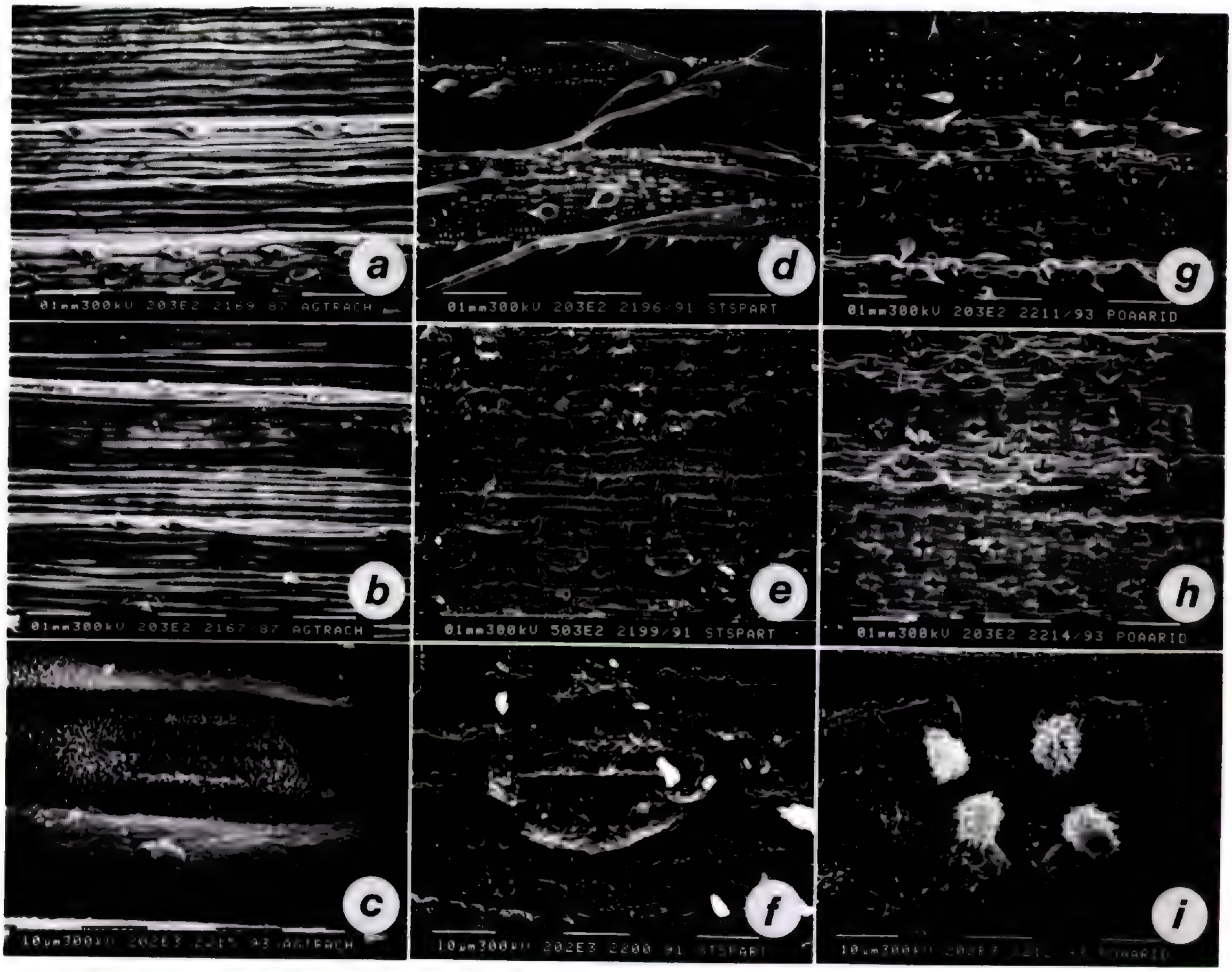

FIGURE 3. Scanning electron micrographs of adaxial (ad) and abaxial (ab) leaf surfaces.—a. *Agropyron trachycaulum*, ad.—b. *A. trachycaulum*, ab.—c. *A. trachycaulum*, ab, stomate.—d. *Stipa spartea*, ad.—e. *S. spartea*, ab.—f. *S. spartea*, ab, stomate.—g. *Poa arida*, ad.—h. *P. arida*, ab.—i. *P. arida*, ad, stomate. Alternating black and white bars indicate the scale (0.1 mm in a, b, d, e, g, h, and 10 μm in c, f, i).

means were not significantly different (*t*-test, Steel & Torrie, 1960). Variation among species in numbers of abaxial stomata was greater in the more drought resistant group (DRI 1–5).

The adaxial surfaces of species exhibiting leaf rolling were strongly ridged or corrugated. An extreme example of this is *Stipa spartea* (Fig. 3d). Stomata were in rows at the bottoms of the furrows between ridges. *Stipa spartea* had 40% of the total stomata located on the abaxial surface, which was relatively smooth and encrusted with cuticular wax (Fig. 3e). *Poa arida* had a less strongly corrugated adaxial surface; however, the stomata on both surfaces were sunken into distinctive pits, which, in the case of the adaxial surface, were surrounded by peculiar wax "balls" and protruding outgrowths of epidermal cells (Fig. 3i). Flat-leaved species, as represented by *Agropyron trachycaulum*, had non-corrugated adaxial surfaces similar to abaxial surfaces (Fig. 3a, b).

Only one species with non-rolling epistomatous leaves, *Calamagrostis canadensis*, appeared among the 39 grasses studied (Table 1). This grass is common in moist to wet sites, sometimes shaded, in the boreal forest. Two other flat-leaved forest grasses, *Bromus ciliatus* and *Elymus virginicus*, and one leaf-roller, *Oryzopsis asperifolia*, also tended strongly toward the epistomatous condition and could be grouped with *C. canadensis*. All other strongly epistomatous species, including *Festuca saximontana*, *F. scabrella*, *Oryzopsis pungens*, *Stipa curiseta*, and *S. richardsonii* have rolling or folding leaves and are found on relatively dry sites in western Canada (DRI 1–5).

Flat-leaved amphistomatous species were mesic forest- or wetland-grasses (DRI 6–10): *Bromus pumpellianus*, *Cinna latifolia*, *Catabrosa aquatica*, and ten other species. All other amphistomatous species had rolling or folding leaves.

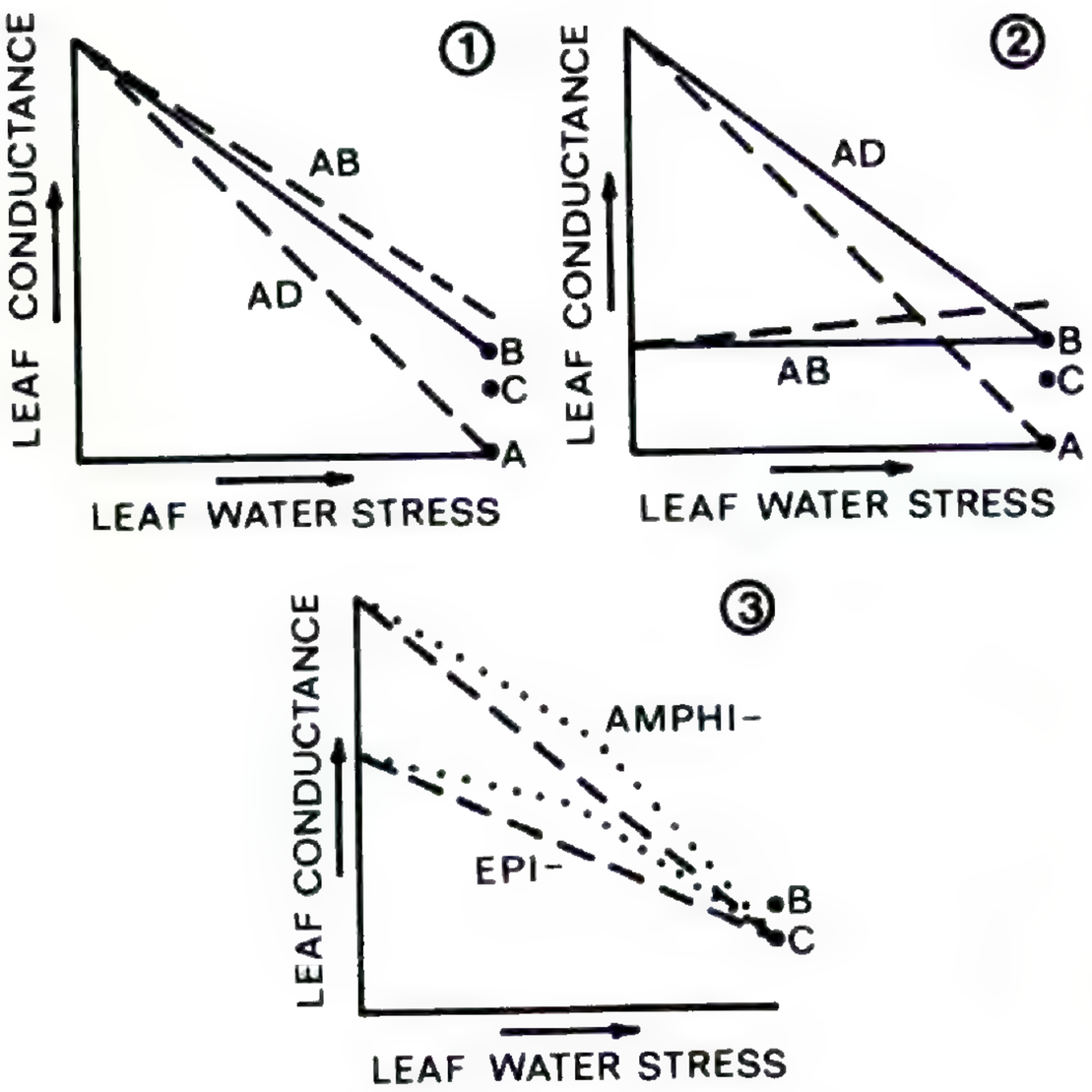

FIGURE 4. Generalized graphs showing relative conductances of amphistomatous and epistomatous leaves in relation to leaf water stress. Solid lines are for flat leaves, dashed lines are for leaves that roll in response to water stress.—1. Amphistomatous leaf, AB = abaxial surface, AD = adaxial surface.—2. Epistomatous leaf.—3. Mean conductances of adaxial and abaxial surfaces in amphistomatous (AMPHI-) and epistomatous (EPI-) leaves. Dotted line shows possible enhanced conductance at a particular stress level due to leaf rolling. See text for further explanation.

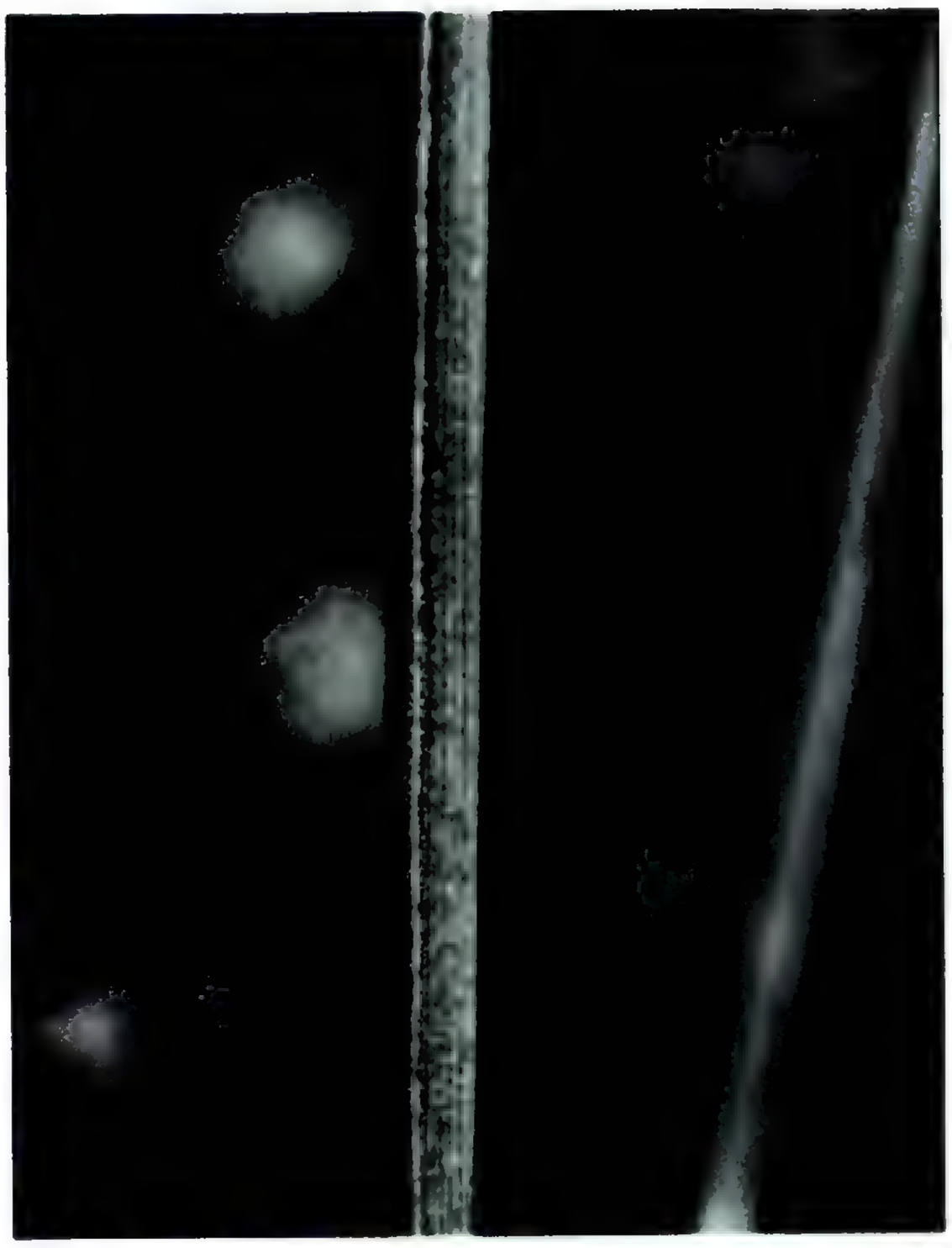

FIGURE 5. Rolled leaf of *Elymus cinereus* photographed several minutes after excision from shoot. Diameter is 3.5 mm.

All those that occurred in habitats with DRI of 1–5 had rolling or folding leaves. A few species from relatively wetter habitats (DRI 6–10) also had leaves that tended to roll: *Scolochloa festucacea* and *Hierochloe odorata* are found in wetlands that can dry out in late season; *Elymus canadensis* and *E. cinereus* occur on sites with wide variation in water availability.

The relationship of leaf type to habitat may be summarized as follows:

(1) Flat amphistomatous leaves—all 12 species with this leaf type occurred only in relatively moist sites.
(2) Flat, epistomatous leaves—four species with this type were from moist, often shaded, forest edge habitats.
(3) Rolling or folding amphistomatous leaves—nine of 13 species in this category were from relatively dry sites.
(4) Rolling or folding epistomatous leaves—five of six species came from relatively dry habitats.
(5) Permanently rolled amphistomatous leaves—the only species in this category, *Oryzopsis hymenoides,* was collected in its typical sand-dune habitat.
(6) Permanently rolled epistomatous leaves—all three species were from dry habitats.

DISCUSSION

The strong trend toward reduction in leaf dimension in grass species from dry habitats (Fig. 1) confirms a well-known trend toward leaf reduction in plants from dry habitats (Daubenmire, 1974). Narrow leaves are more efficient heat exchangers and are less likely to overheat when exposed to drought and high irradiance (Parkhurst & Loucks, 1972; Gates, 1980). Leaf rolling reduces leaf dimension even further, reducing radiation intercepted *per leaf,* and enhancing sensible heat transfer, especially under conditions of free convection (Ripley & Redmann, 1976). Rolling influences latent heat transfer through its effects on (1) leaf temperature, and therefore on water vapor density in the leaf, and (2) boundary layer conductance.

Stomatal distribution is an important factor in determining the degree to which rolling reduces leaf water vapor conductance. A simple, concep-

tual model was devised to help explain how leaf conductance is related to stomatal distribution, leaf rolling, and water stress regime (Fig. 4). The model presented here is meant to aid in interpretation of the observations of leaf characteristics. Hypotheses derived from this analysis should be examined using a quantitative simulation model, and verified by field measurements of leaf conductance.

The model assumes that at low water stress, conductances of the adaxial and abaxial surfaces of the amphistomatous flat and rolling leaves are the same. With greater water stress, rolling increases until complete closure is reached and adaxial conductance drops to zero (Fig. 4-1, point A). Whether rolling completely closes off the adaxial surface is uncertain; however, this seems to be the case for species that I have observed (Fig. 5). The conductance of the abaxial surface of the rolled leaf is considered to be somewhat higher than for the flat leaf, owing to the smaller dimension and thinner boundary layer of the former. At point B, stomatal conductance is zero, and only cuticular water loss occurs from the two surfaces of the flat leaf. Point C represents the average cuticular conductance of the adaxial and abaxial surfaces of the rolled leaf. A complete average curve for the rolling amphistomatous leaf is given in Figure 4-3.

The adaxial surfaces of the flat and rolled epistomatous leaves are assumed to respond in the same way as the amphistomatous types (Fig. 4-2). The abaxial surface has only cuticular conductance, which increases slightly with rolling.

The average whole leaf conductance of the epistomatous leaf is lower than the amphistomatous type, except at high water stress, where they are equal (Fig. 4-3). The average conductance for the upper and lower surfaces (point C) is the same for both the epistomatous and amphistomatous rolled leaves and is lower than the average of the surfaces of flat leaves (point B).

The major reason for decreasing conductance with water stress is stomatal closure. Boundary layer resistance is a relatively small component of total leaf resistance to water vapor transfer, at least in the open canopies typical of dry grassland. Only at maximum water stresses, assuming there is a complete "seal" of the rolled leaf edges, does boundary layer resistance become large (and conductance very small).

Natural selection of leaf form and function must optimize all of the following for any environmental regime: (1) maximum carbon dioxide conductance, (2) minimum water vapor conductance (when water supply is limiting), and (3) leaf temperature (Parkhurst & Loucks, 1972). Cost of constructing a particular leaf form also is a factor in the Parkhurst and Loucks analysis. A rolling-type leaf, with its extensive support tissue and other non-photosynthetic cells, thick cuticle and wax layers, trichomes, etc., must be more "costly" to produce than a simple, flat leaf.

The model (Fig. 4) suggests a hypothesis that rolled epistomatous leaves with their lower total conductance are disadvantageous except in habitats with sustained water stress, where minimization of water vapor conductance and avoidance of leaf overheating are important factors. Some recent data (Cohen et al., 1982) support this idea: The lowest-yielding of several slections of *Festuca arundinacea* had 44% lower abaxial stomatal frequency, and 10% higher adaxial stomatal frequency compared with other selections in field plot studies. Flat amphistomatous leaves would be favored in habitats with lower water stress, where high carbon dioxide conductance is a benefit and water loss is less a problem. Amphistomatous rolling leaves are a "compromise" design selected for in habitats where water availability fluctuates widely on a seasonal or diurnal basis. In this way the contradictory goals of maximizing carbon dioxide conductance and minimizing water conductance can be resolved.

A number of studies suggest that partial rolling might actually be a mechanism to sustain rather than reduce transpiration when evaporative demands are high. For example, Stocker (1972) described *Aristida pungens* as a dune grass with rolled leaves "of highest perfection," which maintains positive photosynthesis and low transpiration even during extreme dry periods. This implies that leaf conductance might be *higher* than for an equivalent unrolled leaf. From data in Willis and Jefferies (1963) it appears that with water stress the transpiration of *Ammophila arenaria* is sustained, even though "inrolling" of the leaves occurs. More recently, O'Toole and Cruz (1980) speculated that leaf rolling shelters the upper surface in such a way that adaxial conductance is higher than abaxial in rolled leaves. Johns (1978) found that conductance of forcibly unrolled leaves of *Festuca arundinacea* was similar to the normally flat leaves of other species. Bennett-Clark (1935, cited in Grieve, 1955) argued that xeromorphic modifications, such as leaf rolling, maintain a moister atmosphere around stomata, thus inhibiting closure and

maintaining conductance. Recently much attention has been paid to the direct response of stomata to humidity (e.g., Losch & Tenhunen, 1981). Rolling might be a mechanism to reduce this sensitivity, permitting higher stomatal conductance under conditions of high evaporative demand. This could result in lowering of tissue water content in rolled leaves, as reported by Rychnovska and Kvet (1963). Higher stress would still result in complete stomatal closure and low conductance. This modified type of response is included in the conceptual model (Fig. 4-3, dotted lines).

Of the 18 species from dry habitats that I examined, only seven (39%) had predominantly epistomatous, rolled or folded leaves. The relative number of species with epistomatous leaves may become larger in consistently drier habitats. When low total leaf conductance is a strong selective advantage, then species with epistomatous leaves may be selected for. This could be tested by measuring stomatal distribution in grass species from more arid habitats than those examined here.

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MIOCENE FOSSIL GRASSES: POSSIBLE ADAPTATION IN REPRODUCTIVE BRACTS (LEMMA AND PALEA)[1]

JOSEPH R. THOMASSON[2]

ABSTRACT

Fossil reproductive bracts of *Berriochloa, Nassella,* and *Paleoeriocoma* of the tribe Stipeae, *Archaeoleersia* of the tribe Oryzeae, and *Panicum* of the tribe Paniceae (Gramineae) were collected from late Oligocene–Miocene strata in central North America, examined, and compared with modern taxa. One objective of these studies was to elucidate the evolution and possible adaptive significance of bract features. *Berriochloa,* the oldest known grass, appears in late Oligocene–early Miocene strata, where it has an indurate, cylindrical anthoecium (lemma and palea collectively) and an elongated, pointed callus. From early Miocene forms of *Berriochloa* two mid-late Miocene lineages evolved, one retaining a cylindrical anthoecium and the other developing a prominently inflated anthoecium. Both lineages retained the elongated, pointed callus. *Paleoeriocoma, Nassella, Archaeoleersia,* and *Panicum* first appear in the late Miocene with anthoecia similar to those of living taxa. The indurate anthoecium of the fossil and related living grasses probably evolved primarily as an adaptation to mammals and insects that use grasses as food. Related living taxa show adaptive mechanisms similar to those of the fossils, although some features such as the strongly interlocking bracts and blunt callus of some species of *Piptochaetium* are a post Miocene development.

The Tertiary deposits of central North American Plains have produced rich and varied floras of considerable paleobotanical interest (Stansbury, 1852; Engelmann, 1876; Cockerell, 1914; Berry, 1928; Elias, 1931, 1932, 1934, 1935, 1942; Frye et al., 1956, 1978; Leonard, 1958; Leonard & Frye, 1978; Frye & Leonard, 1959; Segal, 1965, 1966a, 1966b, 1966c; Skinner et al., 1968; Galbreath, 1974; Diffendal et al., 1982; Voorhies & Thomasson, 1979). Grasses in these floras are found as silicified reproductive bracts or as remains of leaves, stems, and roots and frequently exhibit detailed epidermal features that aid in determining phylogenetic relationships of fossils and their modern counterparts (Thomasson, 1976, 1977, 1978, 1979, 1980a, 1980b, 1984). Fossils described include reproductive bracts assigned to *Archaeoleersia* of the tribe Oryzeae, *Berriochloa, Nassella,* and *Paleoeriocoma* of the tribe Stipeae, and *Panicum* of the tribe Paniceae and leaf fragments assigned to the subfamilies Festucoideae and Arundinoideae.

This paper presents results of my studies of the reproductive bracts (lemma and palea) or bract (lemma) enclosing the mature grain or caryopsis of fossil grasses and their related living taxa. It reviews the geologic and paleoecologic background, summarizes the morphologic features of the fossil and living grasses, examines evolutionary trends among the fossil grasses, and speculates on the adaptive significance of features seen in fossil and living grasses.

GEOLOGIC AND PALEOECOLOGIC BACKGROUND

The late Tertiary (Oligocene–Pliocene) strata of the central part of North America are a widespread group of continental sediments extending from North Dakota and Wyoming to Texas and New Mexico that were deposited principally in fluvial and aeolian environments. They consist of a large variety of sediments including clays, silts, sands, conglomerates, freshwater diatomites, and volcanic ashes and vary in thickness in individual sections from more than 200 m to 1 m. Although some early studies suggested rather simple models of deposition and biostratigraphy, more recent investigations have demonstrated their depositional and biostratigraphic complexity (Bart, 1975; Breyer, 1976, 1981; Skinner et al., 1968, 1977; Swinehart, 1979; Thomasson, 1979; Diffendal, 1980, 1982). Among the most richly fossiliferous Tertiary strata in the world, they contain assemblages of

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TABLE 1. Stratigraphic relationships and ages of late Tertiary strata and study sites in the plains of central North America.

Epoch (Ma)	North American Land Mammal Age (Ma)	Study Sites[a]	Formation
Pliocene	Blancan		
— 5 —	— 4.5 —		
	Hemphillian	85	
	— 9 —	9, 50, 56	Ogallala
	Clarendonian		
	— 11 —		
	Barstovian	56	
Miocene	— 16 —		
	Hemingfordian	64, 65	Sheep Creek
	— 20 —		
		79, 81	Harrison–Monroe Creek
— 24 —	Arikareean		
Oligocene			

[a] Geographic localities: Kansas, west-central (9); Nebraska, west-central (50, 79), northeastern (56), northwestern (64, 65); Texas, northern (85).

fossil plants and animals that have been the subject of numerous taxonomic and biostratigraphic studies for nearly 150 years. Some of the most paleontologically productive of these deposits are, from the oldest to the youngest, the Harrison, Sheep Creek, and Ogallala (including the Valentine, Ash Hollow, and Kimball) Formations. The geographic locations of several major study sites, the general stratigraphic relationships, and ages of the geologic formations and the stratigraphic levels from which fossil grasses have been studied are shown in Table 1. The stratigraphy, biostratigraphy, and lithologic characteristics of each of these formations have been studied extensively, and the reader is referred to these studies for further information (Harrison—Yatkola, 1978; Swinehart, 1979; Sheep Creek—Skinner et al., 1977; Ogallala—Breyer, 1976, 1981; Thomasson, 1979; Swinehart, 1979; Diffendal, 1982). An excellent historical review of the various interpretations of the stratigraphic relationships of these formations is that by Galusha (1975).

The vertebrate faunas found in each of the formations include abundant grazing and semi-grazing cursorial animals such as camels, horses, and rhinoceroses. This suggests savanna or savanna parkland was present in the central plains of North America throughout the late Oligocene and Miocene. Based on the abundance of aeolian sediments in the late Oligocene and early Miocene strata, the environment during this period appears to have been arid to semi-arid (Swinehart, 1979). However, by the middle and late Miocene the environment was more humid and probably subtropical, as indicated by the preponderance of sediments deposited by fluvial processes and by the presence of vertebrates such as large land tortoises and crocodiles in the strata (Holman, 1971; Voorhies, 1971; Thomasson, 1979). The abundance of volcanic ash in the sediments indicates widespread and massive volcanic activity during deposition of all of the formations (Skinner et al., 1977; Yatkola, 1978; Thomasson, 1979; Swinehart, 1979; Voorhies, 1981), but the climatological and perhaps evolutionary effects of this activity have not been explored. Fossil wood with annual rings suggests that wet and dry seasons were probably present throughout the period from the late Oligocene to late Miocene, but the extremes of winter and summer present on the plains today are probably a post Miocene development.

FEATURES OF GRASS ANTHOECIA

In order to reasonably speculate about the adaptive significance of features seen on the bracts of fossil and living grasses it is necessary to re-

TABLE 2. Husk features of Late Tertiary fossil grasses and related living taxa. Explanation of symbols: * = fossil genus; c = obconic, d = cylindrical, f = fusiform, k = biconvex, l = lenticular, n = oblong, s = spheroid, v = obovate; o = absent, + = present; b = blunt, s = sharp; a = papillae, h = hooks, i = microhairs, m = macrohairs, t = "pointless" hooks, p = prickles.

Genus	Shape	Interlocking Lemma and Palea	Callus Type	Surface Structures of the Lemma	Silica Bodies on the Lemma
*Berriochloa**	c, d, n, s, v	o	s	h, m, p	o
Piptochaetium	c, d, n, s, v	+	b, s	h, m, p, t	o
Stipa	d, n	o	s	h, i, m, p	o, +
*Nassella**	f, v	o	b	h, m	o
Nassella	f, l	o	b	h	o
*Paleoeriocoma**	f	o	b	h, m	o
Oryzopsis	f, n	o	b, s	h, i, m, p	o, +
*Panicum**	k	o	b	a	o
Panicum	k	o	b	a	o
*Archaeoleersia**	l	+	b	a, i, p	o
Leersia	l	+	b	a, i, p	+

view the nature and occurrence of the features. Only those taxa represented by both living and related fossil forms will be considered, although discussions of the features are undoubtedly relevant to many other taxa. Summaries of the features of the fossil grasses and their related living counterparts are given in Tables 2 and 3.

SHAPES OF THE ANTHOECIUM

In living grasses the shape of the mature anthoecium is extremely variable, being narrowly to broadly cylindrical or oblong in *Stipa* and some *Piptochaetium*; spindle-shaped, obovate, oblong, or nearly spheroid in *Oryzopsis, Piptochaetium,* and *Nassella*; biconvex in *Panicum,* and lenticular in *Leersia* and some *Nassella.* In early studies the anthoecium shape was thought to be generically distinct, but as Barkworth (1983a, 1983b) and I (Thomasson, 1976, 1979, 1980b) have shown, this is not true. For example, in the genus *Piptochaetium* the shape of the anthoecium varies from elongate, cylindrical in *P. avenaceum* (formerly *Stipa avenaceum*), to obconic in *P. uruguense,* to spheroid in *P. stipoides.* Further, I have suggested that taxa such as *S. viridula* and *S. robusta,* which have been assigned to the genus *Stipa* on the basis of their oblong to cylindrical anthoecia with pointed calli, probably belong in the genus *Oryzopsis* on the basis of micromorphological features (Thomasson, 1981). More studies such as the one conducted by Barkworth (1983b) are needed to determine accurately generic relationships and limits in the Stipeae.

Anthoecium shapes found among the fossil grasses are similar to those found in living forms. Although *Stipa* and *Piptochaetium* are not found as fossils, their common ancestor *Berriochloa* is present and varies in shape from cylindrical to spheroid (Parodi, 1944). Similarly the living grasses *Oryzopsis* and *Leersia* are represented in the fossil record by *Paleoeriocoma* and *Archaeoleersia* respectively, and the shapes are nearly identical (Thomasson, 1980a, 1980b).

TYPES OF CALLI

The callus in grasses is an extension of the anthoecium below the base of the lemma and palea. Generally it is an extension of the lemma, and it may be elongate to short and sharply pointed or blunt (Figs. 1, 2). Commonly the sharply pointed type is associated with an elongate, cylindrical or oblong anthoecium and the blunt type with a more robust, obovate or spheroid shape. Grasses assigned to *Stipa* usually have pointed calli whereas those assigned to *Oryzopsis* and *Nassella* have short, slightly pointed to blunt calli. *Piptochaetium* is the most variable with respect to the callus: elongate and sharply pointed in *Piptochaetium avenaceum* and short and blunt in *P. stipoides* and *P. montevidense.*

The various types of callus found in living grasses were also found in fossil grasses, but their distribution among fossils sometimes differs from that in living grasses. Thus, while calli found on species of fossil *Paleoeriocoma* and *Nassella* were similar to those on species in related, living *Oryzopsis* and *Nassella,* all species of *Berriochloa,* regardless of the shape of the anthoecium, have

TABLE 3. Features of the husks of Miocene fossil grass genera and related living genera of the tribe Stipeae. Explanation of symbols: * = fossil; ** = Thomasson, 1978; o = absent; a = well developed and indurate; b = moderately or weakly developed and not indurate; c = well developed and prominent; d = moderately or weakly developed.

Genus	Palea	Grooved Palea	Raised Lateral Walls on Long Cells**	Spheroid Husks	Long Cells Several Times Longer than Wide	Sharp Callus
*Berriochloa**	a	o	o	c	c	c
Piptochaetium	a	c	c	c	o, c	o, c
Stipa	a, b	o	o	o	o, c	c, d
*Nassella**	o	o	o	o	o	o
Nassella	o, b	o	o	o	o	o
Oryzopsis	a	o	o	o	o, c, d	o
*Paleoeriocoma**	a	o	o	o	d	o

sharply pointed calli. This suggests that the evolution of the blunt callus as found in several species of *Piptochaetium* is a post Miocene event.

INDURATION OF THE BRACTS

In all of the living genera considered during this study, the lemma at maturity was indurate, but the palea was equally indurate in *Leersia, Oryzopsis, Panicum, Piptochaetium,* and *Stipa,* membranaceous in some *Stipa* and rarely some *Nassella,* and absent in most *Nassella.* In any case, at maturity the lemma and palea or lemma alone form a rigid container that encloses the ripe caryopsis (Fig. 3).

Among the fossils, the lemma and palea were well developed and apparently indurate (as judged by the preservation of the bracts) in all taxa except *Nassella,* in which the palea was absent.

INTERRELATIONSHIP OF THE LEMMA AND PALEA

At maturity the lemma and palea or lemma alone form a container for the caryopsis, but this happens in several different ways depending on the interrelationship of the lemma and palea. In species of *Stipa* and *Nassella* with an indurate lemma and a membranaceous palea or no palea at all, the lemma wraps around on itself and forms the rigid anthoecium. In other taxa in which both the lemma and palea are indurate and play a role in the development of the anthoecium, two conditions may occur. First, as in many species of *Stipa* and *Oryzopsis,* the two bracts may simply overlap with the lemma externally, thereby forming the anthoecium (Fig. 3). In the second condition the rigid anthoecium is formed by the physical interlocking of the lemma and palea as in *Leersia, Panicum,* and *Piptochaetium* (Figs. 4, 5). The lemma and palea may be weakly interlocked as in *Panicum* or strongly so as in *Leersia* and *Piptochaetium* in which the lemma interlocks into prominent grooves of the palea (Thomasson, 1976, 1980a).

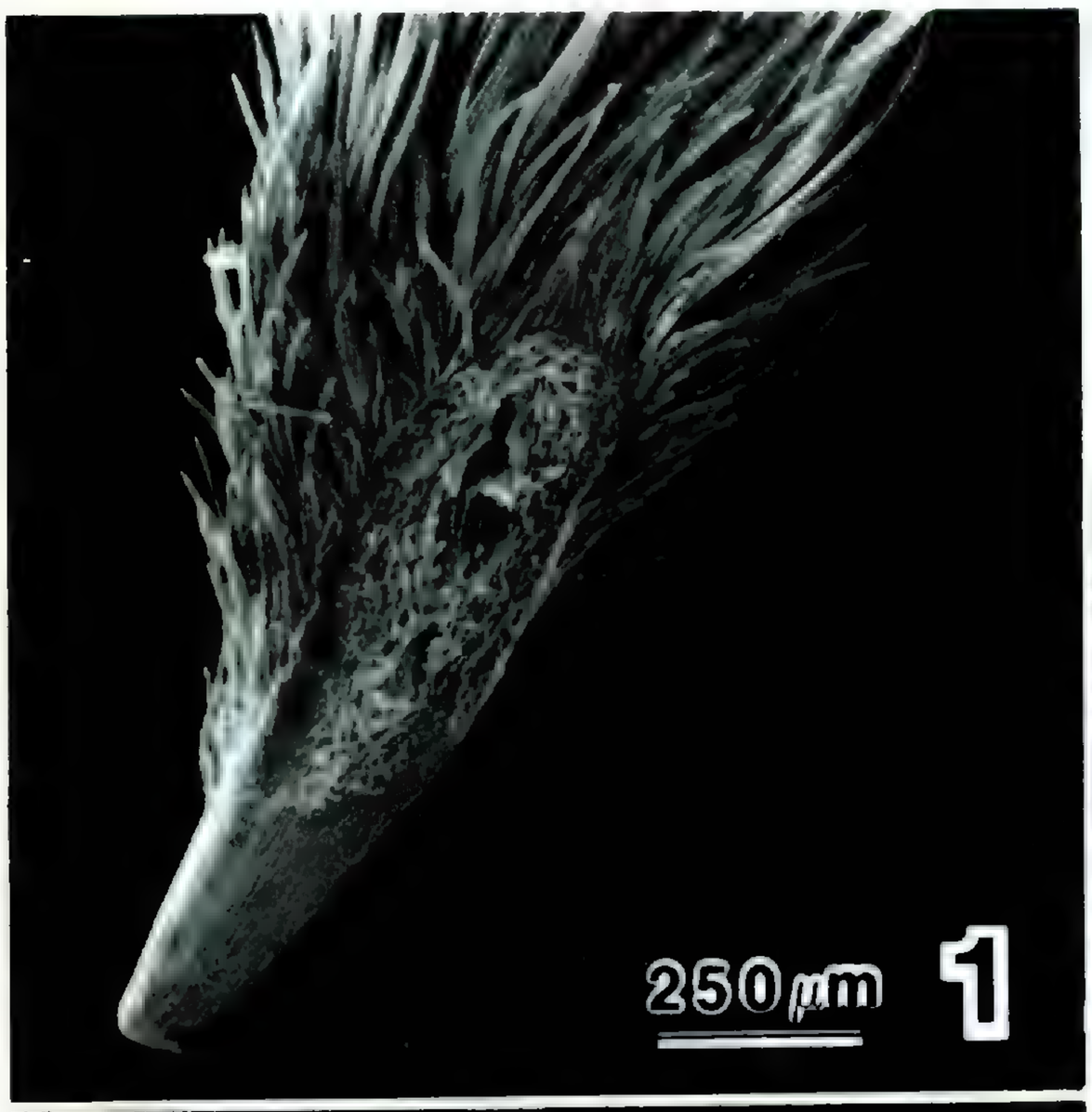
The interrelationship of fossil lemma and palea is the same as in living taxa except the grooved palea of *Piptochaetium* is absent in *Berriochloa* so that this feature apparently evolved after the Miocene. The strongly grooved and interlocked palea found in *Leersia* is present in the related Miocene *Archaeoleersia.*

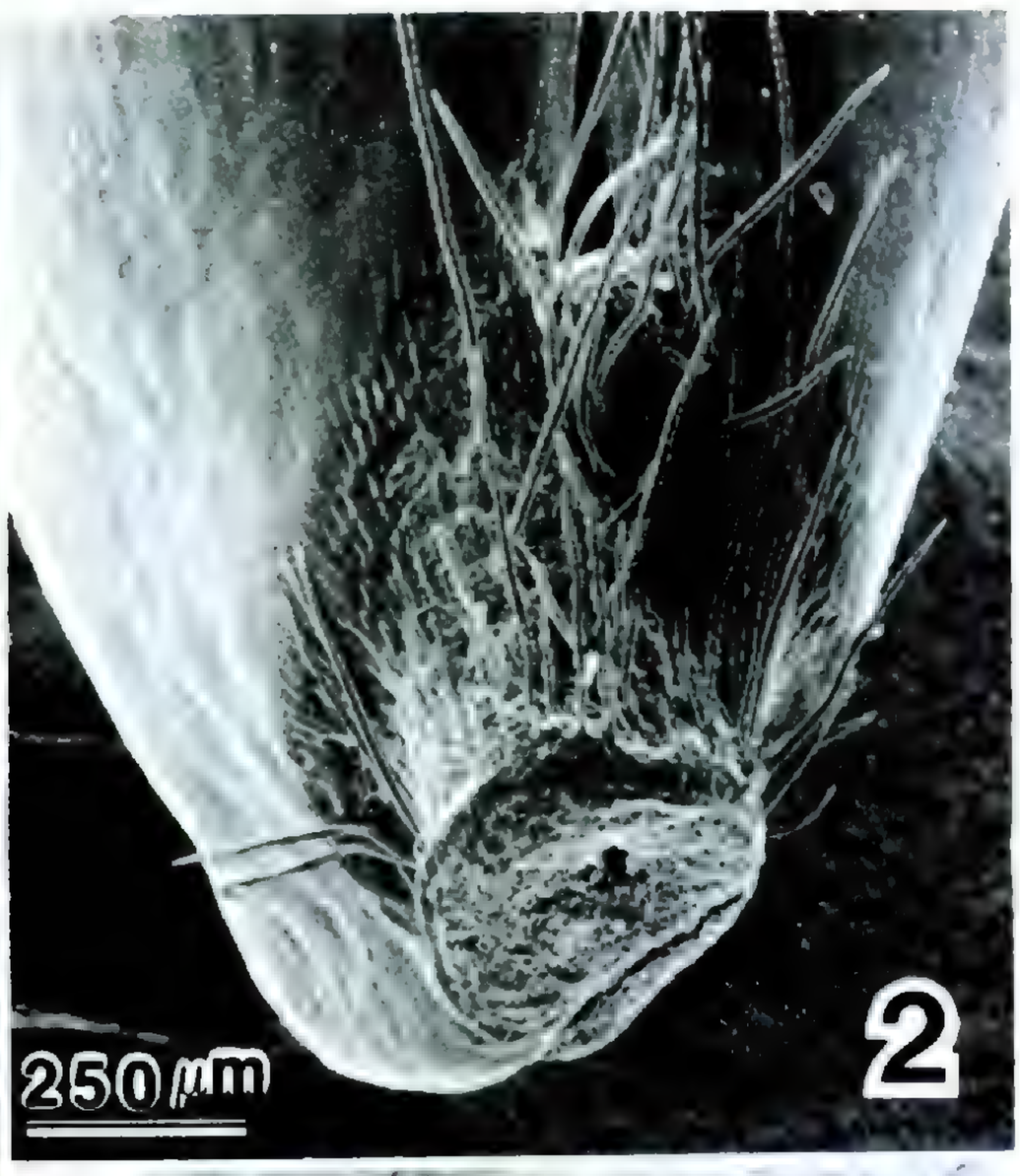
MICROMORPHOLOGICAL STRUCTURES OF THE LEMMA AND PALEA

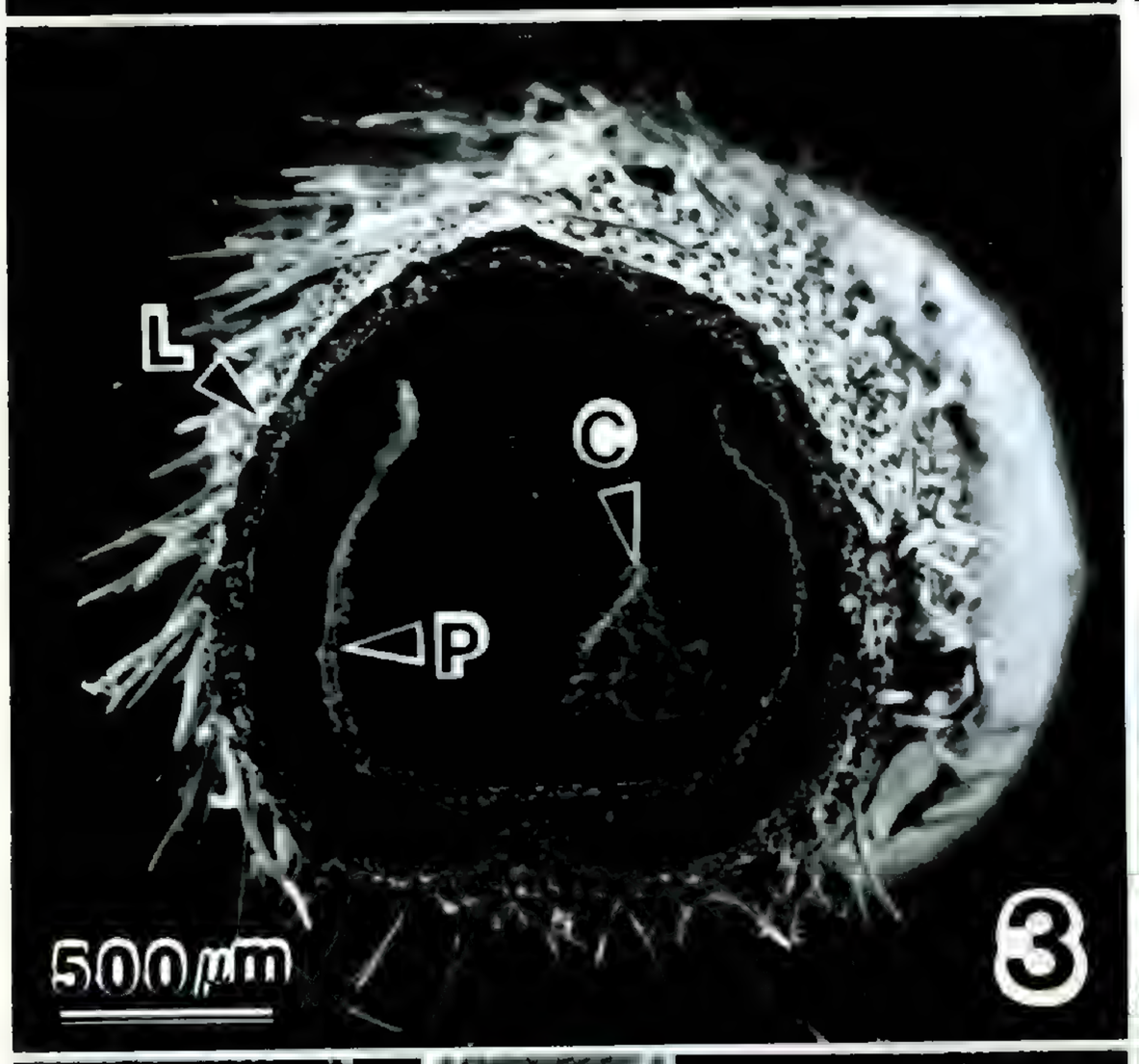
Types of micromorphological structures found on lemmas and paleas of living taxa investigated include macrohairs, prickles, hooks (= barbs, crochet, or crown cells), papillae, silica bodies, and microhairs (see Metcalfe, 1960; Ellis, 1979; or Palmer and Tucker, 1981, 1983 for detailed descriptions of the different types of structures). One interesting variation of these structures is a type of hook found on *Piptochaetium montevidense* in which the point at the apex of the hook

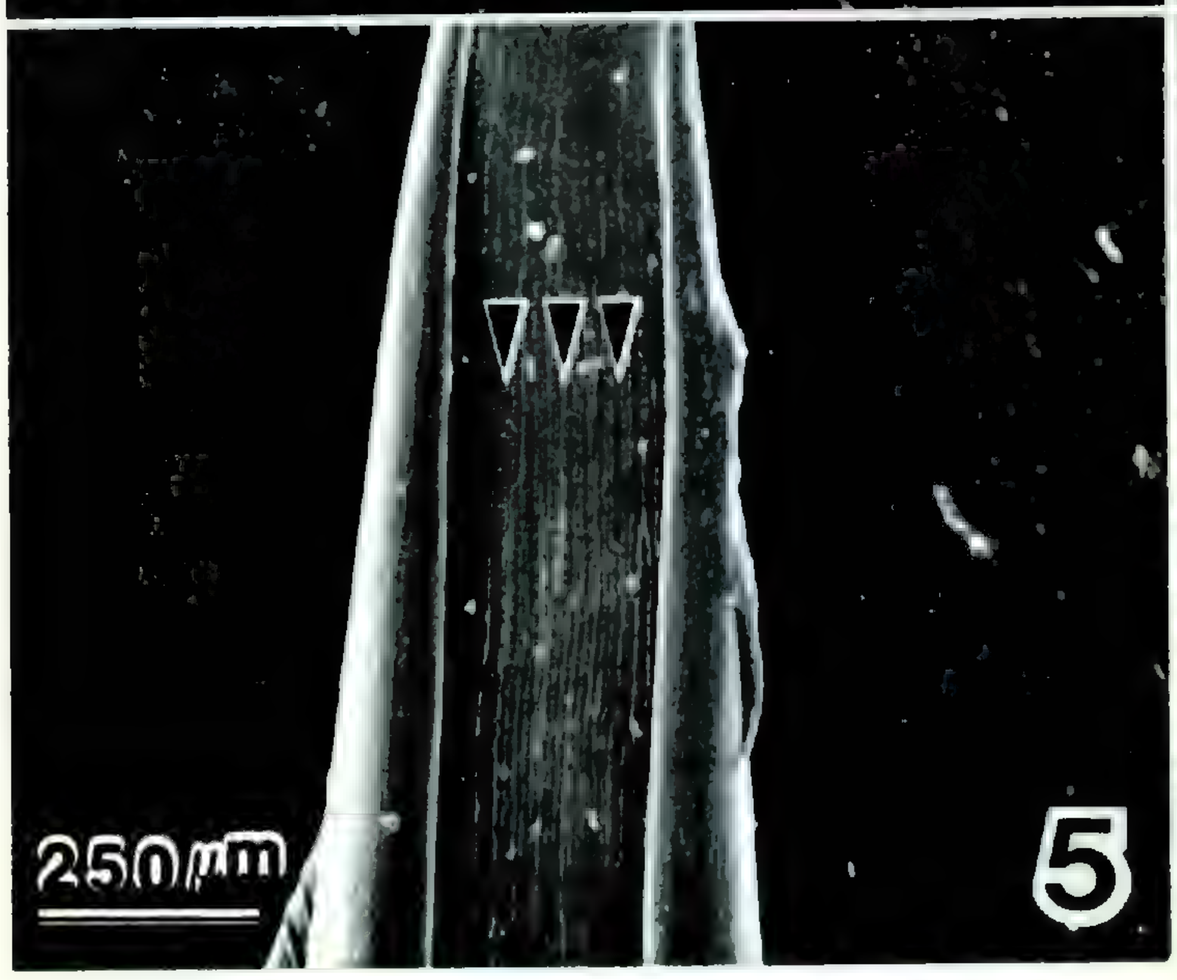
→

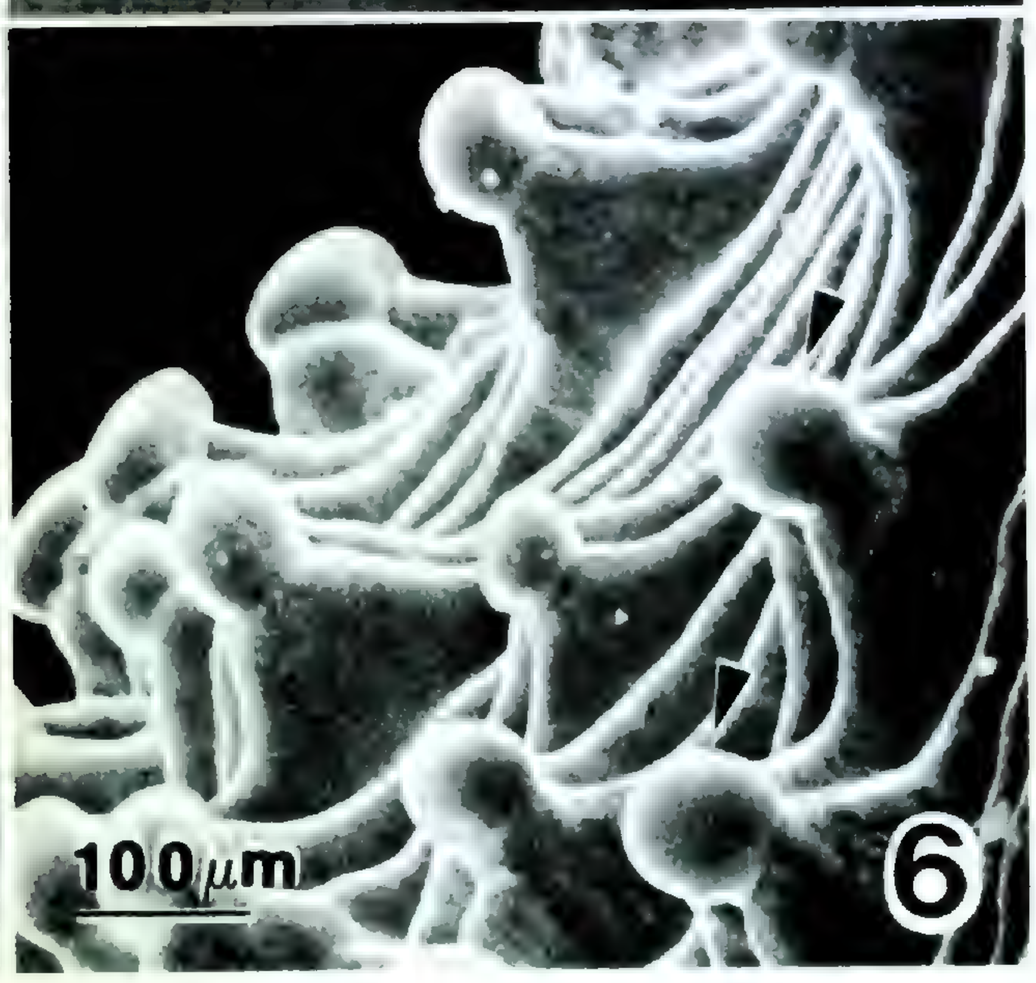
FIGURES 1–6.—1. Elongate, pointed callus of *Piptochaetium avenaceum.*—2. Blunt callus of *Piptochaetium brevicalyx.*—3. Cross section of the mature anthoecium of *Stipa comata* with enclosed caryopsis (C). Note the overlapping relationship of the lemma (L) and palea (P).—4. Cross section of the anthoecium of *Piptochaetium*











bicolor. Observe that the lemma (L) interlocks with the palea (P) in a palea groove (G).—5. Palea removed from the anthoecium of *Piptochaetium avenaceoides* to show distinct medial groove (arrows).—6. Lemma surface of *Piptochaetium montevidense* showing "pointless" hooks (arrows).

is greatly reduced or entirely absent (Fig. 6). While I refer to these structures as "pointless" hooks, I speculate later that, in combination with the anthoecium shape, they actually have an important function in protecting the caryopsis. Except for "pointless" hooks, all surface structures observed on living taxa were also observed on fossil taxa.

EVOLUTIONARY TRENDS IN FEATURES OF THE GRASS ANTHOECIUM

One of the most obvious trends that I and others (Elias, 1942) have observed in fossil grasses is the change in anthoecium shape in the genus *Berriochloa*. The oldest known late Oligocene–early Miocene fossil grasses [Harrison–Monroe Creek (undifferentiated) Formation, 23 Ma] have anthoecia that are elongate cylindrical (e.g., *B. schereri*). These are succeeded in the middle Miocene (Sheep Creek Formation, 17 Ma) primarily by grasses such as *Berriochloa minima*, that have elongate cylindrical anthoecia, although at least two grasses (*B. primaeva* and *B. dawesense*) from this period have more inflated, oblong anthoecia. By the late Miocene (Ogallala Formation, 8–12 Ma) two lines of grasses emerge based on the shape of the anthoecia. In one line (e.g., *Berriochloa communis* and *B. grandis*) the anthoecium is elongate and cylindrical whereas in the second (e.g., *B. glabra* and *B. inflata*) the anthoecium is inflated and obconic to nearly spheroid.

A second trend among fossil grasses is an increase in overall size of the anthoecia in the genus *Berriochloa*. Species found in older strata of the Harrison and Sheep Creek Formations (e.g., *Berriochloa schereri* and *B. minima*) have anthoecia that are predominantly cylindrical to oblong and small (length 1.5–5 mm and width 0.4–1.4 mm), whereas in much younger strata of the Ogallala Formation species (e.g., *B. grandis* and *B. communis*) with similarly shaped, but larger anthoecia (length 3–12 mm and width 0.7–2.5 mm) are common. Likewise, the only species with inflated, obovate to fusiform anthoecia that occur in older strata (*Berriochloa primaeva* and *B. dawesense* in the Sheep Creek Formation) have small anthoecia (length 1.1–4.5 mm and width 0.6–1.4 mm), whereas there are several species (e.g., *B. maxima, B. glabra, B. tuberculata,* and others) with very robust, fusiform to spheroid anthoecia (length 2.5–8 mm and width 2.2–3.5 mm) that are found only in the much younger Ogallala Formation.

A final trend among the fossil grasses is an increasing variety of taxa from older to younger strata. This is true even though thousands of specimens from each stratigraphic level are known. In the oldest levels only the genus *Berriochloa* is known and is represented by two species, whereas in the younger strata of the Sheep Creek Formation as many as seven species of *Berriochloa* are known. In the late Miocene Ogallala Formation an explosion in the numbers of taxa of fossil grasses occurs, with as many as 20 species of *Berriochloa* being known, in addition to species of *Archaeoleersia, Nassella, Panicum,* and *Paleoeriocoma.*

Although exact explanations for the trends among fossil grasses are unknown, it is possible to speculate on their causes and adaptive significance.

I believe that evolution of the two lines of anthoecium shapes (elongate, cylindrical and inflated, fusiform to spheroid) appears primarily to represent a response to the coevolution of grasses with animals and insects that ate the caryopsis as food (see section later in this paper on the adaptive significances of anthoecium features). This suggests that the shape of the anthoecium has limited taxonomic utility (i.e., unrelated taxa may have similarly shaped anthoecia), and this finding has been supported by my studies, at least at the generic level. To illustrate, when the first fossil grasses of the tribe Stipeae were recovered from the High Plains Tertiary strata two taxa, *Stipidium* and *Berriochloa,* were described primarily on the basis of the anthoecium shape, the former having cylindrical anthoecia and the latter having inflated anthoecia (Elias, 1932). However, I have since shown that anthoecium shape alone cannot be used in determining generic relationships in the fossil and modern Stipeae, but rather that a combination of micromorphological and macromorphological features of the anthoecium must be used (Thomasson, 1979, 1981) (Table 3).

I speculate that increasing size of anthoecia is a long term response to foraging insects such as harvester ants. It is well known that these insects collect large numbers of grass anthoecia (Wheeler & Wheeler, 1963; Davison, 1982), and that they select seeds according to size (i.e., the smaller the body length of the forager the smaller the seeds collected) (Davison, 1982). An increasingly larger anthoecium might have reduced foraging on

the caryopsis of species with large anthoecia and thus favored those species with increased survival of caryopses, each of which could potentially germinate and produce a new plant.

Finally, with respect to the increasing variety of taxa, several explanations are possible including increased immigration of new taxa, more complex environments with more diverse ecological niches, or more favorable conditions for preservation (e.g., more alkaline groundwaters resulting in more silica in solution). In the genus *Berriochloa* the increasing variety of species might reflect increasingly diverse responses of grasses to their coevolution with foraging animals and insects.

Adaptive Significance of Anthoecium Features

An important goal of my studies of Tertiary grasses and their living counterparts has been to discern the adaptive significance of the anthoecium features. Based on my studies and observations and those of others, it is possible to speculate on the adaptive significance of grass anthoecium features:

1. *Rigid indurate anthoecium.*
   a) Protection from damage to the caryopsis during ingestion by mammals. Evidence from recent and fossil fecal deposits and from anthoecia associated with skeletal remains (Parodi, 1944; Voorhies, 1974; Thomasson, 1976; Voorhies & Thomasson, 1979).
   b) Protection from insects that feed the caryopsis to larvae. Evidence from both modern and fossil burrows (Wheeler & Wheeler, 1963; Davison, 1982; Thomasson, 1982).
2. *Pointed callus.*
   a) Aids in dispersal of anthoecium with enclosed caryopsis through attachment to the hide or entanglement in the hair of mammals (Parodi, 1944; unpubl. data).
   b) Burial of the anthoecium and caryopsis in the soil (Barkworth, 1983a; unpubl. data).
3. *Blunt callus.* The absence of a sharply pointed callus may facilitate rapid movement of the anthoecium through the digestive tracts of mammals.
4. *Cylindrical anthoecium.* The narrow, elongate anthoecium facilitates burial in cracks in the soil (Barkworth, 1983a; unpubl. data).
5. *Inflated anthoecium.*
   a) In combination with the blunt callus, the inflated shape allows for more rapid movement of the anthoecium through the digestive tracks of mammals (Parodi, 1944).
   b) The inflated shape protects against use by many insects that have great difficulty in moving all other similarly shaped disseminules (Davison, 1982).
6. *Surface structures.*
   a) Pointed surface structures such as hooks may aid in the entanglement of the anthoecium in the hair of animals.
   b) Large pointed features such as macrohairs, especially on the callus, aid in the burial of the anthoecium by making it difficult for the anthoecium to come free once lodged in cracks in the soil (Barkworth, 1983a; unpubl. data).
   c) Blunt, raised structures such as papillae and "pointless" hooks, especially in combination with inflated anthoecia with blunt calli, facilitate rapid movement of the anthoecium through the digestive tracts of mammals.
7. *Grooved palea.* May act as a mechanism to securely lock the lemma and palea together for increased protection of the caryopsis during passage of the anthoecium through the digestive tracts of mammals.

The degree to which anthoecium features are interrelated is particularly interesting. For example, the anthoecium of the South American grass *Piptochaetium montevidense* has a combination of features that include an indurate, obovate anthoecium formed by a strongly interlocking lemma and palea, a short, blunt callus, a lemma surface covered with large "pointless" hooks, and a readily deciduous awn. Rather than asking what the function of any single feature is, the question that I think must be answered is: What is the function of the combination of characteristics observed? For example, common sense suggests that the rigid, indurate anthoecium probably functions in protecting the caryopsis from something. But from what? In order to answer that question and others concerning the adaptive significance of anthoecium features, I have examined evidences from both the past and present, and I have concluded that the principal factor acting on the evolution of many of the features seen on the fossil and living grasses is the co-

evolution of the grasses with animals and insects that ingest (purposely or inadvertently) the caryopsis. In arriving at this conclusion all of the features of the anthoecium have been considered. Thus, in the case of *P. montevidense* the features observed should protect the caryopsis by aiding the rapid movement of the anthoecium through an animal's digestive tract (rounded shape, rough surface, and blunt callus) while preventing damage by digestive juices (indurate, interlocking bracts). Features seen on a grass such as *Stipa comata,* however, would allow for easy burial of the anthoecia in cracks in the soil (cylindrical anthoecium with a hairy, sharp callus and persistent awn) while providing protection to the caryopsis from foraging insects and mammals (indurate, overlapping bracts). Although factors of the environment such as mesic and xeric habitats probably have influenced the evolution of certain features of the anthoecium (e.g., the sharp callus) the features have not been influenced to the degree suggested by Barkworth (1983a).

CONCLUSION

Many features of grasses that have allowed them to be phenomenally successful in competition with other plants, animals, and insects have a long geologic history. The results of my studies of fossil and living grasses have suggested possible explanations of the adaptive significance of many features of grass anthoecia and have provided a better understanding of the evolution of grasses. Whereas most of the fossil history of grasses and the actual origins of many grass features are unknown, the widespread distribution of Cretaceous and Tertiary deposits containing abundant floras provide unlimited opportunities for future exploratory studies on the intriguing question of grass evolution.

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GRAMINOID RESPONSES TO GRAZING BY LARGE HERBIVORES: ADAPTATIONS, EXAPTATIONS, AND INTERACTING PROCESSES[1]

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ABSTRACT

The problem of ascribing adaptive significance to traits that enable graminoids to tolerate or evade ungulate herbivory is examined. Some of these traits may have originally evolved in response to non-grazing selection pressures, thus constituting grazing exaptations rather than true adaptations. The fossil record indicates that semiarid habitats, extensive grasslands, and grazers appeared, interacted, and evolved together. However, several traits that are advantageous in semiarid habitats have beneficial effects for grazed plants. Other traits, such as developmental plasticity, enhance competitive ability in certain environments, but also increase grazing tolerance or resistance. Experiments and simulation modeling showed that defoliation responses are embedded in a network of interacting processes, including photosynthesis, transpiration, nutrient uptake, and resource allocation. Responses and adaptations to defoliation must be interpreted in this context. Although traits may have arisen due to non-herbivorous selection pressures, they may subsequently have been selected, combined, or amplified through grass-grazer coevolution to form species, polymorphic populations, phenotypically plastic individuals, or communities of species that evade, resist, or tolerate herbivory.

Graminoid grazing tolerance and the nearly simultaneous increase of grasses and grazers in the fossil record (Stebbins, 1981) suggest that grasses are adapted to herbivory, perhaps as a result of coevolution. Grasses and herbivores may, consequently, be somewhat mutualistic (Owen & Wiegert, 1981). Graminoid tolerance of herbivory due to continued elongation from the base of the leaf and lateral growth through tillering following defoliation have long been known (Lisle, 1757; Arber, 1934). Interacting physiological and morphological characteristics of graminoids that contribute to such grazing tolerance have been identified (McNaughton, 1979a) and analyzed (Coughenour et al., 1984b, 1985a). However, the origin of present traits in organisms cannot always be attributed to selection pressures of their present environment (Gould & Lewontin, 1979). The current beneficial effect of a trait is actually incidental or secondary if the trait frequency increased in response to another previous selection pressure. Thus, we must distinguish between beneficial traits (aptations) that are only incidentally beneficial (exaptations), and traits that have actually resulted from selection pressures to confer their present benefits (adaptations) (Gould & Vrba, 1982). We should consider alternative non-adaptive hypotheses in any investigation of the presumed adaptive significance of traits (Eriksson et al., 1983).

Evolutionary constraints reduce the variety of evolutionary options available to a species. A trait may be non-adaptive in the sense that it is a necessary consequence of another trait (Eriksson et al., 1983). More fundamentally, individual traits are not in themselves the targets of natural selection. It is the fitness of the whole organism, or interacting system of traits, that determines the outcome of natural selection (Mayr, 1983). This "cohesion of the genotype" results in inevitable compromises among competing demands and a residue of sub-optimal parts that are necessary for the working of the whole (Mayr, 1983). Most plants are in essence metapopulations (White, 1979) of repeating modular units (Harper, 1981). The effect of herbivory on modular organisms differs from the effect of predation on non-modular organisms in that modular organisms survive predation through vegetative reproduction, whereas non-modular organisms do not. Therefore, it is necessary to consider defense against herbivory in a context of other interacting physiological processes and morphometric traits. Factorial experimentation and simulation mod-

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eling are used here to examine interactive processes, causal networks, and possible competing demands that are relevant to herbivory response in perennial graminoids.

Evolutionary History of Grasses and Grazers

The original selection pressures that gave graminoids their current morphological and physiological characteristics can never be absolutely known. However, some insight can be gained by examination of the origins of grasses in relation to grazers in evolutionary time and space. These origins must be related as well to pre-grazing ancestors to determine possible preadaptiveness of traits, and to non-grazing selection pressures such as climate, which may have given rise to grazing exaptations.

Monocotyledons as a broad group are evolutionarily more advanced than dicotyledons, exhibiting neotony as an evolutionary response to extreme environmental conditions, particularly to an aquatic habitat (Takhtajan, 1969). Linear, parallel-veined leaves that grow from their bases arose from modified bladeless petioles, and the sheathing bases of monocot leaves are a consequence of the single cotyledonary structure (Cronquist, 1968). The first monocotyledons probably arose in the Cretaceous period (135–70 Ma) (Raven & Axelrod, 1974).

By the tertiary period (70 Ma) most ancestral grasses had differentiated. Predominantly xerophytic types developed to the south into Africa (Jacques-Felix, 1962). However, there are basically three contrasting theories (Whyte, 1974) regarding the origin of primitive grasses: (1) origin in the humid tropical forests, with increasing evolutionary advancement correlated with greater adaptation to aridity (Bews, 1929); (2) origin in open forest followed by migration into xerophytic zones (Valentine, 1970); (3) origins in mesophytic and xerophytic zones with subsequent mixing of types (Aubreville, 1962; Thomas, 1966). A typical primitive grass may have been a small, low-growing perennial, somewhat tufted, with short leaves, and probably forest-loving (Stebbins, 1972).

Early grasses and hypsodont-toothed mammals first appeared in the fossil record in early Eocene (60 Ma) strata of South America. During the Oligocene (40–25 Ma) several new groups of notungulates appeared in the first open savannahs in South America. In the Miocene (25–12 Ma) horses with more refined hyposodont teeth appeared, and predominated the large herbivore fauna of North America (Stebbins, 1981). Semiarid conditions appeared in South America 20 million years earlier than in North America, but the greater continentality of the North American climate caused more rapid changes in environmental selection pressures (Stebbins, 1981). The Rocky Mountain uplift, and resulting aridity of the Great Plains caused a retreat of forests in late Oligocene and Miocene (30–12 Ma) leaving drought-tolerant grasses and herbs behind (Dix, 1964). Close-grazing bison and sheep arrived in North America from Eurasia in the Pleistocene (3–0.01 Ma) (Mack & Thompson, 1982; Stebbins, 1981). Equidae and Camelidae migrated from North to South America at the end of the Pliocene (3 Ma) or early Pleistocene (Stebbins, 1981).

Existence of grass savannahs in Africa beginning in the Eocene (60–40 Ma) is suggested by the sparse fossil record of this period (van der Hammen, 1983). Poaceous grasses may have entered South America from Africa during the Paleocene (70–60 Ma) or even uppermost Cretaceous (Stebbins, 1981).

In Africa, the Eocene-Miocene (60–12 Ma) was dominated by perissodactyls and proboscideans. Increasing continental elevation was accompanied by increased aridity in the Oligocene (40–25 Ma) (Raven & Axelrod, 1974). Grazing, ruminating bovids appeared first in fossils of the late Miocene (18–12 Ma) in Eurasia and radiated greatly during the Pliocene (12–3 Ma), but they did not invade Africa until late Pliocene (Sinclair, 1983). In the late Pliocene-Pleistocene (4–0.01 Ma) the climate fluctuated in Africa, causing fluctuations in vegetation types and expansion-contraction cycles of savanna habitats. As a result, there was great adaptive radiation in the African large herbivore fauna (Morton, 1972). There may have been significant evolutionary development of grass species at this time (Love, 1972).

Thus, grasses evolved at an early date and existed for quite some time prior to abundant grazing animals. Increasing specialization and adaptations to aridity occurred among grasses subsequently. Extensive grasslands, grazers, and semiarid climates appeared almost simultaneously. This simultaneity makes it difficult to ascertain the original adaptive values of traits that enhance survival under both aridity and grazing.

ADAPTATIONS FOR DROUGHT OR GRAZING?

A number of traits that allow graminoids to evade, resist, or tolerate drought provide similar benefits to plants subjected to grazing. These traits are basal meristems, small stature, high shoot density, deciduous shoots, belowground nutrient reserves, and rapid transpiration and growth.

Linear leaf elongation from an intercalary meristem at the base of the leaf is an ancient trait of monocotyledons. This trait probably made it more feasible for some monocots to maintain intercalary meristems in a protected position at the base of the plant during vegetative growth. Basal meristems, protected by the basal sheath in grasses, may be better able to withstand drought (Barlow et al., 1980). Many perennial grasses have reduced bud height, which is regarded as a means to survive a stressful non-growing season (Raunkaier, 1934). However, primitive grasses adapted to semiarid habitats "probably had already developed enough of a basal intercalary meristem to enable leaves to recover from grazing" (Stebbins, 1972).

Small stature is a well known characteristic of many graminoids that are adapted to more arid habitats. Water and time both impose an upper limit on individual shoot size. In general, however, there is an inverse relationship between shoot size and shoot number (Gorham, 1979). Having many small shoots facilitates rapid response to ephemeral water availability, distributes the risk of drought-induced mortality, and increases the rate of recovery from defoliation. A shorter growth form is also less likely to have a large proportion of its leaves removed by large herbivores.

Deciduous shoots allow perennial graminoids to survive drought by reduction of both transpiring leaf area and shoot maintenance respiration. However, senescent leaves are low quality food items that limit herbivore population sizes (Sinclair, 1975) and, therefore, herbivore impacts. Drought-deciduous leaves are relatively inexpensive to construct compared with leaves of drought-enduring plants (Orians & Solbrig, 1977; Mooney & Gulmon, 1982), and therefore herbivore damage is less costly to the plant. Exportation of nutrients back to perenniating organs during senescence (Williams, 1955) further reduces the impact of herbivory (Mattson, 1980).

Perennial grasses endure the dry season with carbon and nutrient reserves stored in sub-surface crowns and roots. When moisture returns, regrowth proceeds at a rate in excess of current photosynthesis, dependent on upward translocation from reserves. This adaptation to a non-growing season is critical for regrowth following defoliation (Trlica, 1977).

Drought-deciduous perennials that are active only in a wet season should be under strong selection pressure to evolve morphological and physiological traits to maximize production when water becomes available (Orians & Solbrig, 1977). Whereas drought-tolerant shrubs use water slowly when wet and continue to transpire when dry, grasses use water rapidly when wet and cease transpiration when dry. Rapid transpiration implies rapid photosynthesis and growth, which help plants recover from defoliation.

ADAPTATIONS FOR COMPETITION OR GRAZING?

In a competitive environment it is adaptive for a plant to have higher plasticity of root–shoot allocation to enable rapid exploitation of light, or soil water, or nutrient resources, as they become available (Grime, 1977). Rapid shoot regrowth and associated diversion of photosynthate from roots to shoots enables rapid response to changing resource availability. For example, a sudden reduction of leaf area causes a shift from water to light limitation, thus requiring rapid diversion of resources to shoots.

The most primitive grasses were small, and the most general trend in grass evolution has been to increase in size, through increased activity of intercalary meristems (Stebbins, 1972). Through sequential activation of the meristems of stem internodes, the meristems of leaf blades are elevated on culmed shoots. This provides a more effective display of leaf area than does a basal origin of all leaf blades, thereby increasing light competitive ability. Increasing lignification and canopy heights associated with graminoid stem growth reduces or deters herbivory (Stobbs, 1973; Jarman & Sinclair, 1979; van Soest, 1982).

The bunchgrass growth form has been hypothesized to be inherently less resistant to herbivory than more rhizomatous or stoloniferous growth forms, possibly due to coevolution of the latter with large herbivores (Mack & Thompson, 1982). However, the way plant modules are arranged relative to one another may have adaptive significance distinct from herbivory tolerance. Vegetative reproduction by tillering is an efficient method of colonizing open sites. Exten-

sive asexual reproduction also decreases the probability of genotypic extinction (Cook, 1979). A plant with short horizontal internodes and tillers packed in a bunch or tussock grows as an advancing front or "phalanx," forming an impenetrable zone of resource preemption. Plants with vigorous horizontal spreading or tillering, on the other hand, have the "guerilla-like" tactic of spreading over an unoccupied area quickly (Harper, 1981). The guerilla growth form is adaptive for plants that compete for space in early successional stages or disturbance sites. Once established, however, protection against invaders is more advantageous. The guerilla-phalanx dichotomy involves a trade-off of resource investment inherent in lateral versus horizontal growth.

Several other traits may allow rapid colonization of open space and increased competitive ability in early successional environments (Bazazz, 1979). These include rapid growth rate, non-light-saturated photosynthetic rate, rapid transpiration and photosynthesis, and reduced sensitivity to decreased water availability. These traits may enable better recovery from defoliation as well.

Defensive Chemistry—Does It, Should It, or Can It Occur in Grasses?

Lignin and silica both reduce palatability; however, it is likely that their primary functions in grasses are non-defensive. Silica reduces digestibility in some grasses, increases it in others, invariably wears down herbivore teeth, and can cause kidney stones (van Soest, 1982). Silica concentrations are sometimes higher in more heavily grazed plants, genotypes or species (McNaughton & Tarrants, 1983; Brizuela, 1985), but this might be taken as evidence either for or against defensive utility. Defoliation induces elevated silica levels in individual plants of some grasses (McNaughton & Tarrants, 1983) but not of others (Cid, 1985). Although invertebrate herbivory is deterred by silica, deterrence of ruminant herbivory has not been demonstrated. Lignin is indigestible, and it can reduce the digestibility of associated carbohydrates (van Soest, 1982). However, both silica and lignin impart rigidity to the cell wall and prevent wilting when cell water contents decrease, as during mild droughts. Xerophytic plants generally have thicker cell walls and are more lignified (Sinnott, 1960). Lignin (Higuchi, 1981) and silica (Russel, 1973) enable terrestrial plants to develop upright forms and be resistant to environmental stress and disease. Thus, grasses that grew in drier, more open habitats evolved firmer and more siliceous leaves, which probably prompted the evolution of hypsodont dentition among grazers (Stebbins, 1981).

Non-lignin phenolic compounds could affect ruminant herbivory of grasses. Tannins and flavones have been isolated from East African grasses (Field, 1976); nevertheless, these species are important forage for native ruminants. Terpenoids occur in another African grass, *Cymbopogon excavatus* (Field, 1976). Regrowth is grazed but mature plants are avoided. Flavonoids and coumarins also occur (Wong, 1973). These compounds have not been shown to deter ruminant grazing.

Grasses lack the variety of toxic chemicals that deter herbivory in dicotyledons. Alkaloids have been isolated from only 21 grasses out of 8,000 examined (Culvenor, 1973). The only alkaloid-bearing grasses that have been shown to affect ruminants, however, are *Phalaris tuberosa, Lolium perenne* (Culvenor, 1973), and *Festuca arundinacea* (Bush et al., 1970). Cyanogenic compounds were detected in only two of 16 grasses (Gibbs, 1974); however, these have not been shown to affect ruminants.

Ruminal microflora are able to degrade a number of otherwise defensive compounds before they reach the stomach. It has been hypothesized that pregastric fermentation originally evolved because it could detoxify secondary compounds in browse plants (van Soest, 1982). Although some tropical grasses contain oxalates that inhibit nutrient absorption by the non-ruminant digestive system of horses (Blaney et al., 1981), the microflora of ruminants degrade the oxalate before it reaches the stomach (Allison et al., 1977). Rumen microflora of domestic sheep have been shown to detoxify alkaloids (Dick et al., 1963) and toxic isoflavones (Nilsson et al., 1967). Several wild ruminants commonly feed on the poisonous fruit of the East African herb *Solanum incanum* L. (Pratt & Gwynne, 1977).

Thus, some chemical constituents do, and therefore can, defend grasses from herbivory, at least to some extent. However, the effectiveness of chemical defenses is limited by the ability of rumen microflora to degrade them. Although lignin and silica have non-defensive functions, they may reduce palatability enough to decrease se-

TABLE 1. Summary of clipping effects on growth and photosynthesis of a short sedge, a mid-grass, and a tall-grass subjected to factorial variations in clipping height (cm) and frequency (d). Compared to unclipped controls, there were stimulations (+), inhibitions (−), and no differences (0).

	K. nervosa	*T. triandra*	*H. filipendula*
Height of plant	10–25	50–120	100–150
Clipping regimes	2, 5 cm/2, 7 d	3, 6 cm/3, 7 d	10, 15 cm/7, 14 d
Aboveground growth			
Total	+	−	−
Tillering	−+[d]	0	0−[a]
Leaf elongation rate[b]	+	+	+
Residual leaf area	−+[d]	−	−
Belowground growth			
Root growth	−0[c]	−	0
Crown growth	−+[d]	−	0
Photosynthetic rate	+−[e]	−+[f]	+
Stomatal conductance	+−[e]	0	+
Internal conductance	0	−+[f]	+
Water status	+[g]	0	+[h]

[a] Inhibited in 14 d, no effect in 7 d clipping treatments.
[b] Short-duration measurement mid-way through experiment.
[c] Inhibited in 2 d, 2 cm treatments.
[d] Inhibited in 2 cm, stimulated in 5 cm treatments.
[e] Stimulated in 2 cm, inhibited in 5 cm treatments.
[f] Inhibited in 3 d, stimulated in 7 d treatments.
[g] Soil water conservation.
[h] Plant water conservation.

lection pressure for other defensive compounds. The benefits of chemical defenses are further reduced by other, morphological or physiological, traits that enable deterrence, tolerance, or evasion of herbivory.

INTERACTIVE PROCESSES AND MORPHOMETRIC TRAITS IN THREE SERENGETI GRAMINOIDS

The responses of grasses to defoliation are imbedded in and determined by a network of interactive physiological processes and morphometric traits (McNaughton et al., 1982). Intensive laboratory experiments with three Serengeti graminoids (McNaughton et al., 1983; Wallace et al., 1984; Coughenour et al., 1985a, 1985b) elucidated this causal network. The short-, mid-, and tall-statured species represented a range of habitat aridity in the Serengeti ecosystem of northern Tanzania.

Qualitatively different responses to defoliation were exhibited by the three species (Table 1). Total aboveground growth, residual leaf area, and tillering were stimulated by clipping only in the short-statured species. However, leaf elongation rate was enhanced in all three species. In turn, clipped yield was significantly correlated with leaf elongation rate in all species. Positive photosynthetic responses to defoliation, mediated by stomatal and internal leaf conductances, compensated for reduced leaf area consistently in the tall-statured species and variably in the short- and mid-statured species. This prevented negative belowground growth responses in the tallest species. Belowground growth was correlated with residual leaf area and tiller number in all species. In general, the tallest species had the most homeostatic response, but the underlying adjustments were the most complex.

Water status of the short and tall graminoids was improved by defoliation. Water additions affected growth in both species and photosynthesis of the latter, suggesting that responses to defoliation were partially mediated by water.

Variations in habitat aridity and light competition exert differential selection pressures upon plant growth form that subsequently influence defoliation responses. The inherent tendencies of shorter-statured species to allocate shoot growth in the horizontal direction via tillering, and for taller-statured species to allocate in the vertical direction via leaf elongation, largely influenced

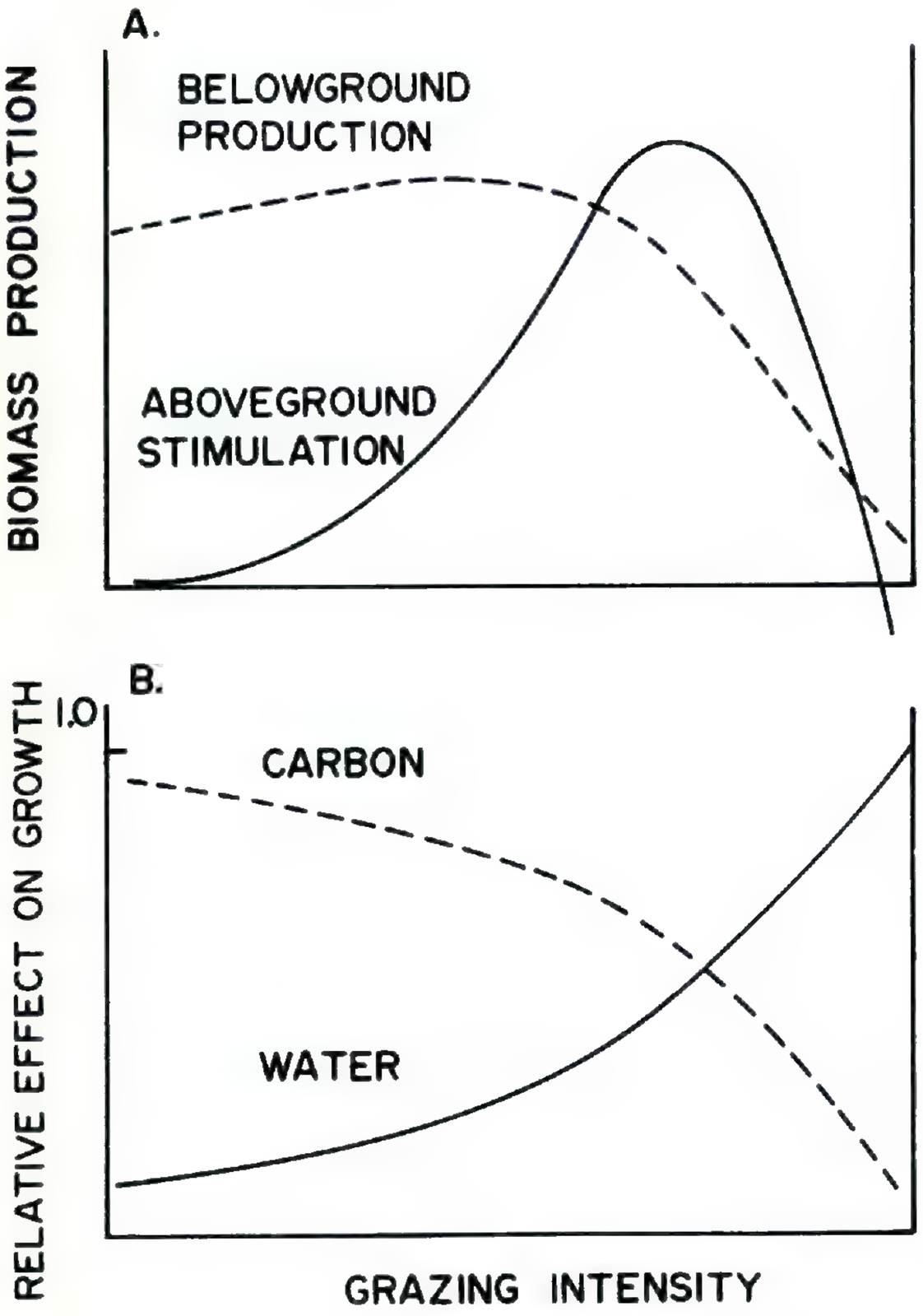

FIGURE 1.—A. The relationship between aboveground biomass stimulation, belowground productivity, and grazing intensity in simulated grasses.—B. The effects of water and carbon on growth, plotted against grazing intensity on the simulated plants. Effects are multiplicative in the model. (Adapted from Coughenour et al., 1985a.)

which of these mechanisms was the more important defoliation response. Similarly, shorter species had inherently greater root/shoot and crown/shoot ratios, that influenced plant responses via the impacts of root biomass on nutrient uptake and crown biomass on nutrient storage and meristem production.

Additional experimentation with *Kyllinga nervosa* has revealed that plant nitrogen relations and grazing responses are highly interactive. Nitrate and ammonium had differential effects on plant responses to clipping, while clipping stimulated uptake rates of both ions (Ruess et al., 1983). Urea nutrition increased material flows to grazers and to plant reproduction, while clipping and urea together resulted in stimulated leaf and flower production, thus establishing a positive feedback from grazers to plants to grazers (Ruess & McNaughton, 1984). Furthermore, grazing affected the balance of several other plant

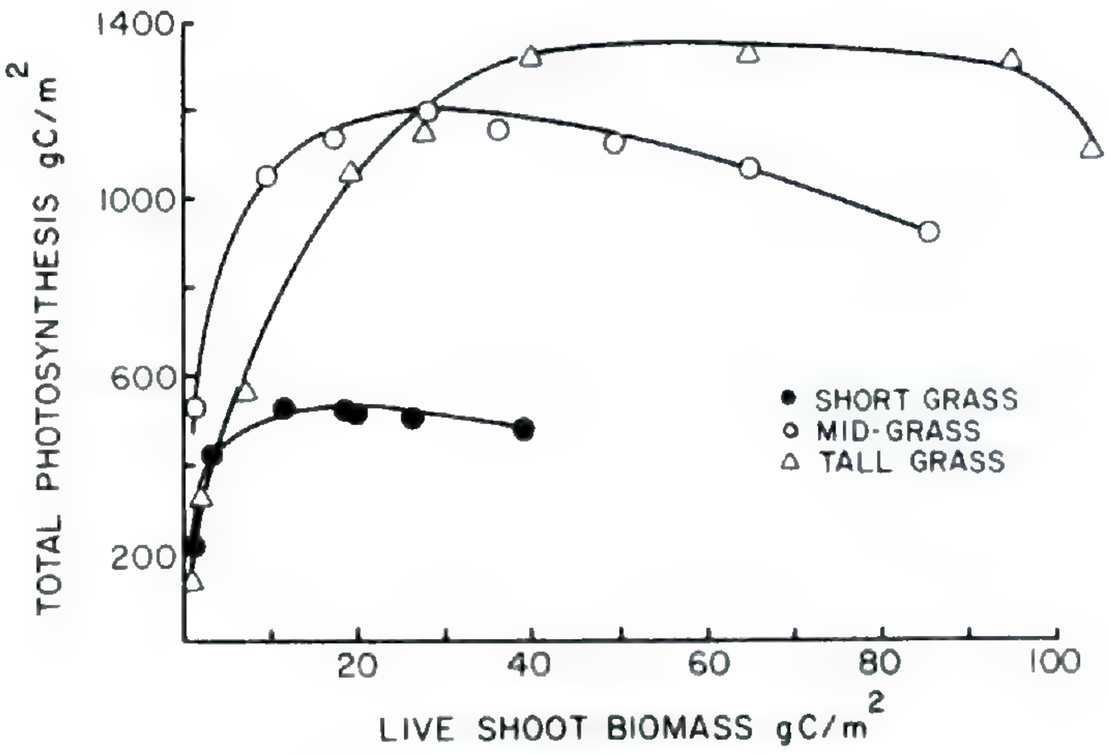

FIGURE 2. Total photosynthesis over a single growing season versus average live shoot biomass of simulated short-, mid-, and tall-grasses. Each point represents a different grazing regime. (Data from Coughenour et al., 1985a.)

nutrients via clipping and nitrogen source (Ruess, 1984).

MECHANISTIC SIMULATION ANALYSES OF CLIPPING RESPONSES

A simulation model was constructed (Coughenour et al., 1984a) that incorporated morphological and physiological aspects of graminoid growth hypothesized to play a role in plant response to defoliation. The model simulated physiological processes that controlled carbon, water, and nitrogen uptake rates and allocations within the plant. The model simulated meristem types and numbers, tissues types and masses, and canopy geometry. Simulation experiments were performed with short-, mid-, and tall-grasses subjected to various clipping heights and frequencies (Coughenour et al., 1984b; Coughenour, 1984).

Response surfaces of yield to grazers (clipped yield) versus grazing height and frequency indicated that shorter graminoids were optimally defoliated at greater frequencies than taller graminoids, primarily because a large number of small shoots reach their maximum sizes more rapidly than a small number of large shoots. Maximum aboveground productivities were achieved at intermediate grazing intensities (Fig. 1A) when aboveground growth was maximally stimulated. Belowground growth was depressed little at low to moderate grazing intensities but declined rapidly at higher grazing intensities. Greater photosynthetic rates lessened reductions in belowground growth. The aboveground growth response to grazing intensity was unimodal pri-

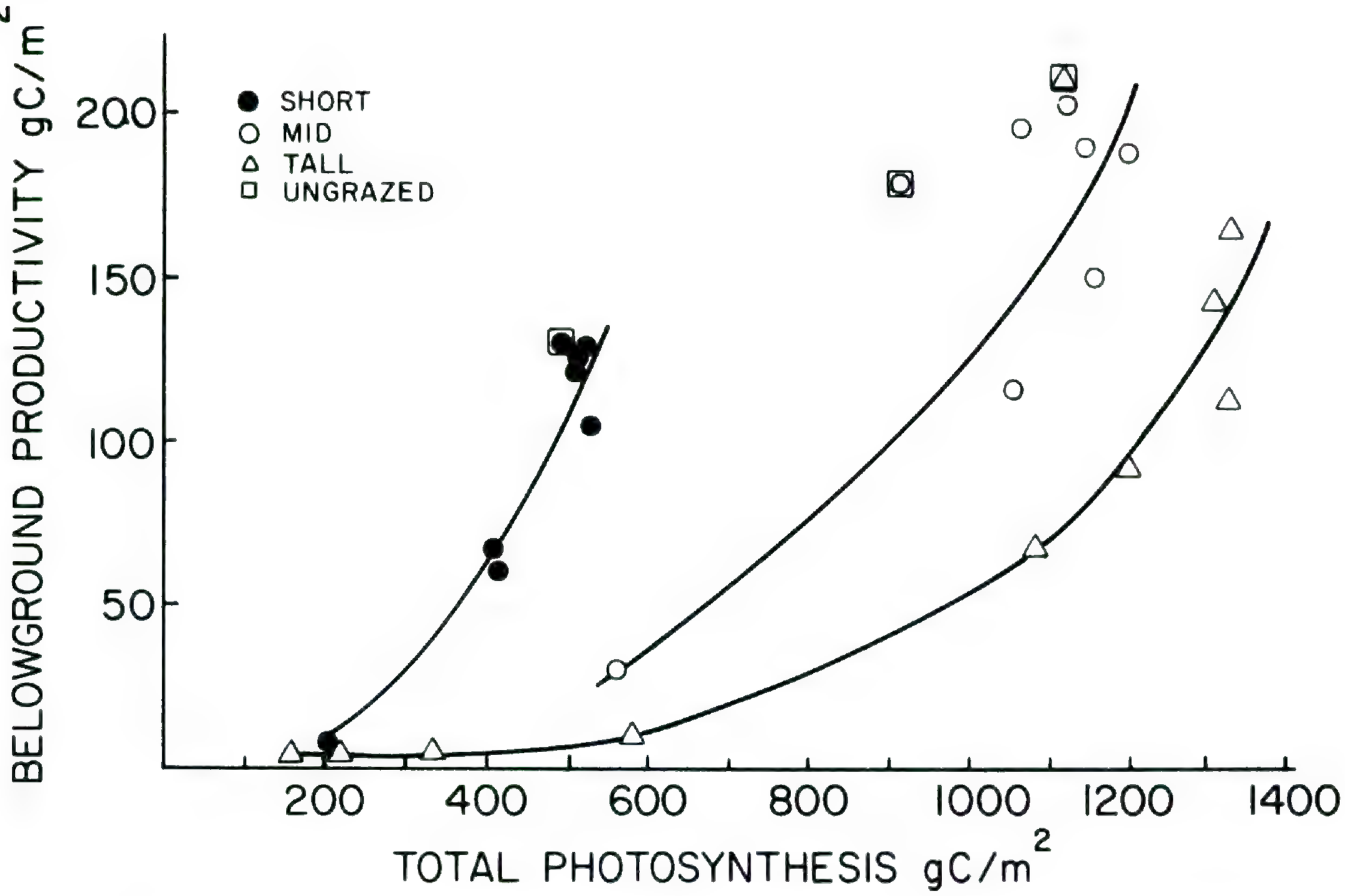

FIGURE 3. Total belowground productivity versus total photosynthesis of simulated plants for a single growing season. These are the same simulations as in Figure 2.

marily because relative water availability increased while relative carbon availability decreased as grazing intensity increased. Total available photosynthate decreased as more was removed by defoliation, but total transpiration and rainfall interception decreased.

Total photosynthate production was maximal at intermediate levels of live shoot biomass (Fig. 2). The increase in photosynthesis was greatest at low levels of shoot biomass, indicating the critical dependence on leaf area at higher grazing intensities. At higher shoot biomass levels an increase in shoots had little or no impact on total photosynthesis because photosynthetic rate per unit leaf area decreased. Total photosynthesis was maximized at lower shoot biomass levels in shorter grasses. Photosynthetic rates of grazed plants were stimulated by grazing. Light and water limitations on photosynthesis were lessened as greater quantities of water and light were available to each unit of leaf area of grazed plants.

Shoot morphology affected the relationship between total photosynthesis and belowground productivity as grazing regimes were altered (Fig. 3). The tall-grass exhibited a non-linear response because more photosynthate was allocated to shoots at low levels of total photosynthesis. The tall-grass produced the lowest quantity of belowground growth with a given quantity of photosynthate because it diverted a greater fraction of photosynthate to fewer, taller, and more lignified shoots. Clipped mid- and tall-grasses had much less belowground growth per unit of photosynthate than corresponding unclipped plants, while clipping did not have this effect on the short-grass.

The effect of shoot morphology was tested with the model by interchanging shoot morphologies of short- and tall-grasses (Table 2). All parameters regulating shoot growth, including shoot number, type, and size, tissue types, and growth rates, were reversed while the remaining biotic and abiotic parameters were held constant. The shoot system of the short-grass had at least twice as many meristems; however, tall-grass maximum individual shoot growth rates were several times higher, and the shoots could grow roughly three to four times larger.

Placing a tall-grass shoot system on the short-grass decreased above- and belowground productivities in all grazed plants. Only aboveground production of ungrazed plants was in-

TABLE 2. Effect of reversing shoot morphology between short- and tall-grasses on above- and belowground production (g/m^2).

Grazing Experiment	Aboveground Production			Belowground Production		
	Ungrazed	Moderate	Severe	Ungrazed	Moderate	Severe
Control	35	116	97	140	112	62
Short-grass with tall-grass shoots	46	84	24	118	94	7
Control	214	512	90	301	158	8
Tall-grass with short-grass shoots	196	419	509	353	324	82

creased. The interchange was especially harmful to severely grazed plants. Aboveground production of the ungrazed tall-grass was depressed by the short-grass shoot morphology, but belowground production was increased because less photosynthate was required by the smaller shoots. (Of course, the experiment did not account for reduced light competitive ability of shorter shoots.) When severely grazed, the tall-grass with short shoots performed considerably better.

Because shorter grasses had greater densities of smaller tillers, defoliation at a given height removed proportionately less foliage, and foliage below the grazing height was more concentrated. Grazing stimulated tillering and converted sparse, tall canopies into shorter ones with denser concentrations of younger, high quality foliage in both the model and in reality (McNaughton, 1976, 1984).

Modeling has explicitly shown that grazing responses are the result of interactions between morphological traits and physiological processes, and that the traits, the processes, and the interactions are, conversely, affected by grazing.

ADAPTATIONS IN INDIVIDUALS, POPULATIONS, SPECIES AND COMMUNITIES

The importance of plant form in grazing response has been demonstrated both through experimentation and modeling. Shorter grasses had greater densities of smaller tillers, so defoliation at a given height removed proportionately less foliage, and foliage below the grazing height was more concentrated. However, morphological shifts to grazing-resistant forms can occur within individuals, populations, or communities. Grazing stimulates tillering, and convertes a sparse, tall canopy into a shorter "grazing lawn" that has a denser concentration of younger, higher quality forage (McNaughton, 1984). Grazing lawns can result from phenotypic plasticity. This was simulated by the model, and shown in controlled experimentation discussed above. Phenotypic responses to grazing are reversed when grazing ceases (Quinn & Miller, 1967).

Another type of grazing lawn can be induced through long-term repeated grazing. Prostrate or dwarfed growth forms, often with a high ratio of basal to culmed meristems, may exist as infrequent ecotypes in ungrazed polymorphic populations. Recurrent, localized grazing may then increase the predominance of grazing-resistant ecotypes in the local sub-populations (Stapledon, 1928; McNaughton, 1979b, 1984; Detling & Painter, 1983; Detling et al., 1985), and the population as a whole would then be a mosaic of genetic variability. Alternatively, somatic mutations during asexual reproduction may facilitate evolution of genets and mosaics of genetic variability (Whitam & Slobodchikoff, 1981). Thus, a third type of grazing lawn could be comprised of plants that are inherently shorter, but also phenotypically plastic (McNaughton, 1984).

Finally, by reducing leaf area, opening up the canopy, creating small disturbance sites, and generally reducing the survival of grazing-intolerant species, grazing may alter competitive relationships in plant communities (Watkin & Clements, 1978; Edroma, 1981). In a grazed plant community lateral resource investment is more important, and shorter species may be favored where taller species would otherwise be competitively superior.

Thus, it is necessary to distinguish the impacts of grazing on individual plants from impacts on localized shifts in the distribution of ecotypes in a population, or species in a community. Since phenotypic plasticity is heritable (Bradshaw, 1974) and since polymorphism can be induced through disruptive selection, either could include examples of true grazing adaptiveness. However,

one must show that the grazing-resistant forms of plastic individuals are usually or only induced by grazing, that polymorphisms with grazing-resistant ecotypes only occur where there is, or was, periodic grazing, or that grazing ecotypes comprise more heavily grazed patches of a mosaic. In the case of non-plastic individuals or non-polymorphic populations, a trait can clearly be attributed to grazing selection pressure only if it is always more predominant, or if it only exists in reproductively isolated populations that are, or were, regularly grazed.

CONCLUSIONS

Grasses and large grazing herbivores evolved together. However, it is difficult to show which graminoid traits arose or are solely maintained by grazing. Part of the difficulty, of course, is that we are unable to determine from the fossil record the precise origin of graminoid traits in relation to herbivore evolution. Extant grasses do withstand, avoid, or deter grazing, yet this does not constitute sufficient evidence for the selection of traits through coevolution with herbivores. I have given a number of examples of possible exaptations, or traits that could have arisen through non-herbivorous selection pressures, but which nevertheless confer benefits to grazed plants.

Either adaptive or exaptive traits may be more frequent among grazed (or ungrazed in the case of deterrence or avoidance) populations or species. If such a trait originally arose through non-herbivorous selection, but is now maintained in the gene pool of a population by grazing, or becomes more apparent in patches of grazed plants through differential survival, the trait should be considered truly adaptive. Similarly, phenotypic plasticity that is maintained by grazing is adaptive irrespective of original selection pressure.

Grasses differ markedly from dicotyledons in their lack of chemical defenses against herbivory. High concentrations of lignin and silica deter herbivory of grasses, but their primary functions are probably structural support and drought resistance. Ruminant microorganisms may make chemical defenses ineffective, and the array of other non-chemical means of coping with or avoiding herbivory may make chemical defenses unnecessary or non-cost-effective.

It is well worth speculation, in view of the novelty and potential importance of the concept, to admit that moderate grazing could have positive long-term effects on grasses (Owen & Wiegert, 1983). Perennial grasses persist for hundreds of years by vegetative reproduction, and moderate grazing can increase vegetative reproduction (McNaughton, 1983a). Thus, grazing can stimulate fitness. If so, natural selection would tend to encourage moderate herbivory of grasses. The lack of chemical deterrents and the high degree of adaptation or exaptation to herbivory among grasses support this possibility.

Experiments and simulation analyses showed that graminoid grazing responses are embedded in a context of interacting physiological processes and morphometric traits. Available water in the native habitat largely determines maximal stature and growth rate. In more mesic environments light competition and thus vertical growth are more important, leading to taller stature and less frequent optimal defoliation regimes. These constraints on plant form and function comprise an aptational context for graminoid responses to herbivory. Conversely, herbivory affects the responses of grasses to their abiotic environment. Therefore, it is necessary to explain defoliation responses in a systems context when referring to adaptive value.

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THREE NEW SPECIES OF *CHUSQUEA* (GRAMINEAE: BAMBUSOIDEAE)[1]

LYNN G. CLARK[2]

ABSTRACT

Chusquea pohlii, C. latifolia, and **C. serpens** are described from Central and South America. Observations on bud morphology and branch development in *Chusquea* are included. Bud morphology provides a new set of vegetative characters invaluable in separating species of *Chusquea*. The bud complement in *Chusquea* consists of one dominant central bud subtended by 2-numerous, smaller subsidiary buds. The number and arrangement of the buds are variable and seem to be species-specific. The bud complement of each of the new species is illustrated and described. Infravaginal branching, found in several *Chusquea* species, including those described here, is defined and contrasted with extravaginal branching, typical of the majority of species in the genus.

Among the woody bamboos, *Chusquea* Kunth has long been recognized as a large and diverse genus. McClure (1973) and Calderón and Soderstrom (1980) included over 90 species within the genus, but according to my observations the count is nearer 120 species. Early descriptions of *Chusquea* species (e.g., Nees von Esenbeck, 1835; Munro, 1868; Hackel, 1903; Pilger, 1905) focused primarily on spikelet morphology. More recently McClure (1973) and Soderstrom and Calderón (1978a, 1978b) recognized the importance of vegetative features in distinguishing among species in *Chusquea,* but interspecific variation of bud and branch complement morphology in the genus has received little detailed study. My work has shown that the bud complement provides a new set of vegetative characters invaluable in separating species, and that there is greater variability in patterns of branch development than has been previously attributed to *Chusquea.*

The bud complement in *Chusquea,* according to McClure (1973: 69), consists of "separate primary buds of two size categories in constellate insertion, the smaller ones usually many (rarely only 2)." Although this fundamental bud morphology is shared by all members of the genus, the number and arrangement of the buds are highly variable and seem to be species-specific. Two representative bud complements are illustrated in Figure 1. The sheath scar is the line of attachment of the culm leaf. The nodal region is delimited below by the sheath scar (nodal line), and above by the supranodal ridge, which may or may not be prominent. The largest, or dominant bud is the central bud, and the smaller subtending buds are called subsidiary buds (McClure, 1973; Soderstrom & Calderón, 1978a, 1978b). In the chusqueoid bud complement, all the buds are of the same (primary) order. The term "subsidiary" is used here in the sense of McClure (1973) to indicate only that the buds so described are smaller than the central bud. As defined by Foster and Gifford (1974), subsidiary buds also could be called collateral buds. The dimorphism between the central and subsidiary buds in *Chusquea* is striking and sets this genus apart from all other bamboos.

Two types of central buds are found in *Chusquea.* The triangular type, exemplified by *C. serrulata* Kunth (Fig. 1A), is very common and like those of other bamboos. The bud is erect and roughly triangular in outline, and the winged prophyllum is easy to distinguish. The circular type of central bud, as seen in *C. liebmannii* Fournier (Fig. 1B), is more or less circular in outline, projecting outward horizontally from the culm. The prophyllum is atypical, apparently lacking wings. I have observed circular central buds in only eight or nine species of *Chusquea* and not in any other bamboo genera.

Extravaginal branching, in which the emerging branches break through the base of the culm sheath proper (Fig. 2A), is typical of *Chusquea*

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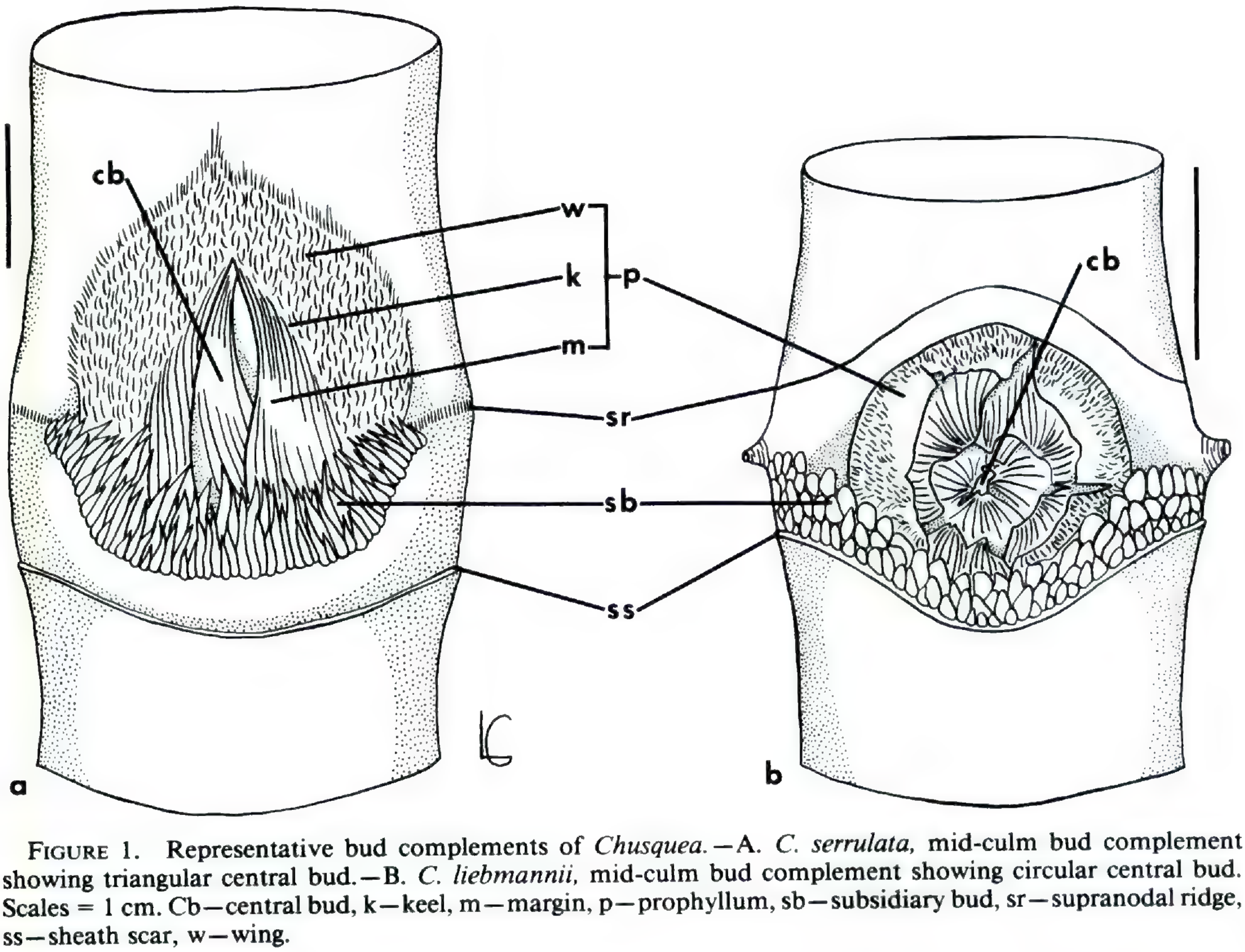

FIGURE 1. Representative bud complements of *Chusquea*.—A. *C. serrulata,* mid-culm bud complement showing triangular central bud.—B. *C. liebmannii,* mid-culm bud complement showing circular central bud. Scales = 1 cm. Cb—central bud, k—keel, m—margin, p—prophyllum, sb—subsidiary bud, sr—supranodal ridge, ss—sheath scar, w—wing.

(Soderstrom & Calderón, 1978b). The girdle, a horizontal band of elastic, usually persistent tissue at the base of the culm sheath in some bamboos (McClure, 1973), usually is not well developed in species of *Chusquea* that exhibit extravaginal branching. However, I have observed in several species of *Chusquea,* including the three species described in the present paper, that the girdle is prominent, forming a sometimes asymmetrical band of tissue up to 1.5 cm wide at the base of the culm sheath. The girdle usually is persistent, even after the culm leaf separates from it and falls away. In contrast to extravaginal branching, here the developing subsidiary branches emerge through the girdle without rupturing the culm sheath (Figs. 3F, 4E). Occasionally, as the branches mature, the culm sheath becomes ruptured to a certain extent, particularly if its overlapping edges are fused at the base (Fig. 3F). I am designating this pattern of branch development "infravaginal," a term suggested to me by Cleofé Calderón. It is clear that this type of branching is derived from the extravaginal pattern by means of the expansion of the girdle, but the distinction between extravaginal and infravaginal branching is taxonomically useful and a parallel, descriptive term is necessary. Infravaginal branching is known in only one other bamboo genus, the Asiatic *Dinochloa* Büse (Dransfield, 1981). In both *Chusquea* and *Dinochloa,* infravaginal branching is correlated with a climbing, viny habit.

The first of the three species described here is named in honor of Dr. Richard W. Pohl of Iowa State University, who has devoted much of his career to studying the grasses of Costa Rica. It is fitting that this Costa Rican endemic commemorate Dr. Pohl's many years of field work in that country and his long-standing interest in the bamboos. Notes of the late Dr. F. A. McClure, filed in the Hitchcock and Chase Grass Library of the Smithsonian Institution (U.S. National Herbarium), show that he considered the second of these three species to be distinct, based on the presence of just two subsidiary buds subtending the central one. Because of the unusual branch complement, he tentatively proposed that this species be included in a new genus. It is evident that his notes and descriptions were at best preliminary; he used at least three different

FIGURE 2.—A. Extravaginal branching in *Chusquea serrulata,* scale = 1 cm (based on *Calderón et al. 2989*). B–F. *C. pohlii.*—B. Inflorescence, scale = 1 cm.—C. Spikelet, scale = 1 mm.—D. Bud complement, scale = 1 cm.—E. Leafy branch, scale = 1 cm.—F. Culm leaf, scale = 1 cm (B–C based on *Croat 36232*; D–F based on *Clark & Clark 275*).

provisional names (of which I chose the most descriptive) for the same entity. Three agrostologists (J. R. Swallen, T. R. Soderstrom, and R. W. Pohl) recognized, apparently independently, that the third species described here was distinct, but the provisional names used would be invalid and no adequate description was ever provided.

1. Chusquea pohlii Clark, sp. nov. TYPE: Costa Rica. San José: along the Interamerican Hwy. between Km 44–45, closer to Km 45, 2,190 m, 27 Feb. 1982, *Clark & Clark 275* (holotype, ISC; isotype, US). Figure 2B–F.

Culmi scandentes, arcuati, usque ad 3 cm diam., usque ad 15 m longi. Folia culmorum persistentia, longior quam nodus sequens extensa, 21–47.6 cm longa: vaginae triangulares, connatae basi, plerumque confertim pubescentia basi, 18.5–39.2 cm longae, 5.4–10.5 cm latae basi, vagina plerumque 5.5- vel 7.5-plo longior quam lamina, externae hispidae, internae sparsim hispidae; laminae persistentes, triangulares, apicibus acuminatis, 2.5–8.4 cm longae, scabrae; cingulum asymmetricum, prominens non nisi prope gemmam. Nodi ad culmum medium gemma centralis singularis rotundata subtenta a (2–)4–9(–12) gemmis parvioribus subaequantibus. Ramificatio infravaginalis. Folia 4–6 in complemento: vaginae hispidae; laminae lineares-lanceolatae, apicibus acuminatis, basibus attentuatis-rotundatis, 14–25.6 cm longae, 1–2.3 cm latae, scabridiusculae superne, glabrae inferne, inferme tessellatae; ligula interna elongata, asymmetrica, (7–)11–30 mm longa. Inflorescentia angusta, paniculata, 21–30 cm longa; rhachis plus minusve complanata, puberula; rami appressi, angulati, puberuli. Spiculae lanceolatae, 6.8–9 mm longae, leviter falcatae. Glumae 2: gluma I squamiformis, 0.5–0.6 mm longa, enervis; gluma II squamiformis, 0.8 mm longa, enervis. Lemmata sterilia 2: lemma sterile I triangulatum, apiculatum, 3.1–4.5 mm longum, 5-nerve; lemma sterile II lanceolatum, apiculatum, 4.1–5.1 mm longum, 5-nerve. Lemma fertile lanceolatum, apiculatum, 6.6–7.6 mm longum, 7-nerve. Palea lanceolata, bicarinata, apiculata, 6.4–7.7 mm longa, 4-nervis.

Culms scandent, to 3 cm diam., to 15 m long, arching. *Internodes* terete, often shallowly sulcate above the central bud on more mature culms, solid, 22–36 cm long, scabrous-hispid below node. *Culm leaves* persistent, usually extending past the next node, 21–47.6 cm long, chartaceous to cartilaginous; sheaths triangular, fused for 2.3 cm above the base, 18.5–39.2 cm long, 5.4–10.5 cm wide at base, usually 5.5–7.5 times, occasionally only 3–4 times, as long as the blade, abaxially hispid but hairs deciduous with age so the sheath often seems scabrous only, adaxially shiny and sparsely hispid toward the apex or sometimes the whole upper half hispid, the margins glabrous, the base often densely pubescent; blades persistent, triangular, 2.5–8.4 cm long, abaxially scabrous, adaxially glabrous and shiny, the apex acuminate, the margins glabrous; girdle asymmetrically developed, prominent only in the region of the bud complement where the sheath scar dips markedly forming a flap through which the lowermost subsidiary branches emerge; inner ligule a short, stiff rim, 1–2 mm long; outer ligule lacking. *Nodes* only slightly swollen, at mid-culm with one circular central bud subtended by (2–)4–9(–12) smaller subequal subsidiary buds. *Branching* infravaginal, central bud rarely developing but sometimes rebranching when developed; lowermost subsidiary buds developing first and emerging through the girdle, the upper ones developing shortly thereafter and emerging through the sheath, forming leafy branches 24–39 cm long, which do not rebranch. *Foliage leaves* 4–6 per complement; sheaths carinate, hispid but often glabrous just below the pseudopetiole and toward the margins, the overlapping margins ciliate; blades linear-lanceolate, 14–25.6 cm long, 1–2.3 cm wide, L : W = 9 : 16, the adaxial surface scabrid and not tessellate, the abaxial surface glabrous and weakly tessellate, the apex acuminate, the margins serrulate, the base attenuate-rounded; pseudopetiole more or less distinct, 2–5 mm long; outer ligule a conspicuous, stiff rim 0.5–2 mm long; inner ligule elongate, asymmetrical, (7–)11–30 mm long, chartaceous. *Inflorescence* a narrow panicle 21–30 cm long; rachis puberulent, one side slightly rounded, the other ridged; branches appressed, arising only from the ridged side of the rachis, angular, 5–6 cm long at the base of the panicle, puberulent; pedicels 1–4 mm long, angular, pubescent. *Spikelets* lanceolate, 6.8–9 mm long, slightly falcate. *Glumes* 2; glume I scale-like, 0.5–0.6 mm long, glabrous, nerves lacking; glume II scale-like, 0.8 mm long, apically obtuse, abaxially pubescent, nerves lacking. *Sterile lemmas* 2; sterile lemma I triangular, 3.1–4.5 mm long, apiculate, abaxially pubescent on the upper half, adaxially pubescent just below the apex, marginally ciliate toward apex, 5-nerved; sterile lemma II lanceolate, 4.1–5.1 mm long, apiculate, abaxially pubescent on the upper half, adaxially pubescent just below apex, marginally ciliate toward apex, 5-nerved. *Fertile lemma* lanceolate, 6.6–7.6 mm long, apiculate, abaxially scabrous-pubescent on the upper half, adaxially pubescent just below apex, marginally ciliate toward apex, 7-nerved. *Palea* lanceolate, 2-keeled, sulcate only toward the apex, 6.4–7.7 mm long, apiculate, abaxially scabrous-pubes-

cent between the keels, otherwise scabrid toward apex, 4-nerved. *Lodicules* 3; 1.5–1.9 mm long, the posterior lodicule narrower than the anterior ones, all ciliolate on the upper margins. *Stamens* 3; anthers linear, 3.3–3.9 mm long. *Ovary* glabrous. *Fruit* unknown.

Representative specimens examined. COSTA RICA. ALAJUELA: Km 15–16, N of San Ramón, *Pohl & Clark 14115* (CR, ISC). CARTAGO: Tapantí Hydroelectric Reserve trail along Río Dos Amigos, 23 June 1976 (fl), *Croat 36232* (MO, US); Alto Patillos, NE of Tapantí, along road to Turrialba, *Pohl 14139* (CR, ISC); at hydroelectric dam, canyon of Río Grande de Orosi, S of Tapantí, *Pohl & Selva 12886* (ISC, MO). HEREDIA: Volcano Barba, wet submontane forest, at end of road, *Booth 161* (US); Route 9, S of the Vara Blanca intersection, between Km 28 & 29, *Clark & Clark 277* (ISC, US); Alto del Roble, Río Las Vueltas, ca. 10 km NNE of Heredia, *Pohl & Gabel 13676* (ISC). PUNTARENAS: Monteverde, along forest road in forest preserve, *Pohl & Pinette 13246* (F, ISC, MO). SAN JOSÉ: along road N of Cascajal, N of Río Cascajal, *Pohl 14101* (CR, ISC); Parque Nacional Braulio Carillo, S boundary, 2 km S of Bajo de Hondura, *Pohl & Clark 14104* (CR, ISC).

This bamboo has solid culms and multiple independent buds at each node, thus placing it in *Chusquea,* where it is distinct enough to merit specific recognition. Pohl (1980, 1983) has referred to this species as the "Tapantí population" of *Chusquea* and *Chusquea "hispidissima,"* respectively. *Chusquea pohlii* is distinguished by its rather thick, coarse, clambering culms, hispid culm and foliage leaf sheaths, subsidiary branches that do not rebranch, long ligules, and spikelets with the sterile lemmas extending approximately one-half the spikelet length. This species has been collected only in the cloud forests of Costa Rica at elevations of 1,500 to 2,600 m, where it can form large colonies in disturbed areas.

The peculiar bud complement of this species is one of its most distinctive features. The central bud is circular in outline rather than triangular (Fig. 2E), and when it develops, the resulting branch initially diverges nearly 90° from the main culm. Usually four to nine smaller subsidiary buds subtend the central bud. As the subsidiary branches develop, they too diverge strongly, becoming geniculate and bending outward, away from the central bud.

2. **Chusquea latifolia** Clark, sp. nov. TYPE: Colombia. Tolima: El Libano a Murillo (Km 11 al 22 de la carretera), subpáramo en el Alto de Peñones, 2,200–2,950 m, 20 July 1947 (fl), *García-Barriga 11259* (holotype, US; isotype, COL). Figure 3.

Culmi scandentes, usque ad 1.5 cm diam., usque ad 40 m longi. Folia culmorum pro longitudine internodia extensa, 17.8–30 cm longa, pubescentia ad juncturam vaginae et laminae: vaginae persistentes, triangulares, connatae basi, 15.2–26.5 cm longae, usque ad 8.5 cm latae basi, multo longior quam lamina, scabrae vel interdum pubescentes; laminae deciduae, triangulares, apicibus acuminatis, 1.1–3.5 cm longae, externae scabrae vel interdum glabrae, internae pubescentes; cingulum prominens, usque ad 1.5 cm longum, pubescens. Nodi ad culmum medium gemma centralis singularis triangularis subtenta a 2 gemmis parvioribus subaequantibus. Ramificatio infravaginalis. Folia 5–9 in complemento: laminae lanceolatae, apicibus acuminatis, basibus rotundatis vel rotundatis-truncatis, 13.3–32.1 cm longae, 3–8.5 cm latae, glabrae superne, glabrae inferne, inferme tessellatae; ligula interna plerumque conspicua, rotundata vel truncata, (1–)2–15 mm longa, plerumque pubescens. Inflorescentia angusta, paniculata, 20.5–42.5 cm longa; rhachis complanata, glabra; rami appressi, secundi, angulati, glabri. Spiculae ovatae-lanceolatae, 8.2–12 mm longae, leviter falcatae. Glumae 2: gluma I triangulata, apice rotundatis, 0.5–1.3 mm longa, enervis; gluma II ovata-lanceolata, apiculata, 2.4–2.5 mm longa, 3- vel 5-nervis. Lemmata sterilia 2: lemma sterile I ovatum-lanceolatum, apiculatum, 3.2–4.2 mm longum, 7- vel 9-nerve; lemma sterile II ovatum-lanceolatum, apiculatum, 4.4–6.5 mm longum, 7-nerve. Lemma fertile ovatum-lanceolatum, naviculare, apiculatum, 8–10.6 mm longum, 9- vel 11-nerve. Palea ovata-lanceolata, bicarinata, sulcata, non apiculata, 8.3–9.6 mm longa, 6- vel 8-nervis.

Rhizomes leptomorph. *Culms* viny, scandent, to 1.5 cm diam., to 40 m long, often trailing for part of the length. *Internodes* terete to slightly laterally compressed, solid, 25–39 cm long, glabrous to scabrous or pubescent just below the nodes. *Culm leaves* extending almost the length of the internode, 17.8–30 cm long, pubescent at the juncture of the sheath and blade, chartaceous; sheaths persistent, triangular, fused to 2.5 cm above the base, 15.2–26.5 cm long, to 8.5 cm wide at the base, at least 9 times as long as blade, scabrous or sometimes pubescent; the margins ciliate near the apex; blades deciduous, triangular, 1.1–3.5 cm long, abaxially scabrous or sometimes glabrous, adaxially pubescent, the apex acuminate, the margins ciliate; girdle usually well developed, to 1.5 cm wide, pubescent, forming a flap through which the branches emerge, often disintegrating before the rest of the culm leaf; inner ligule a short, ciliolate rim; outer ligule lacking. *Nodes* only slightly swollen, at mid-culm with one triangular central bud subtended by two smaller subequal buds. *Branching* infravaginal, central bud sometimes developing into a robust branch more or less equal in size to the main culm and rebranching; subsidiary buds 2, developing into leafy branches 17–66 cm long

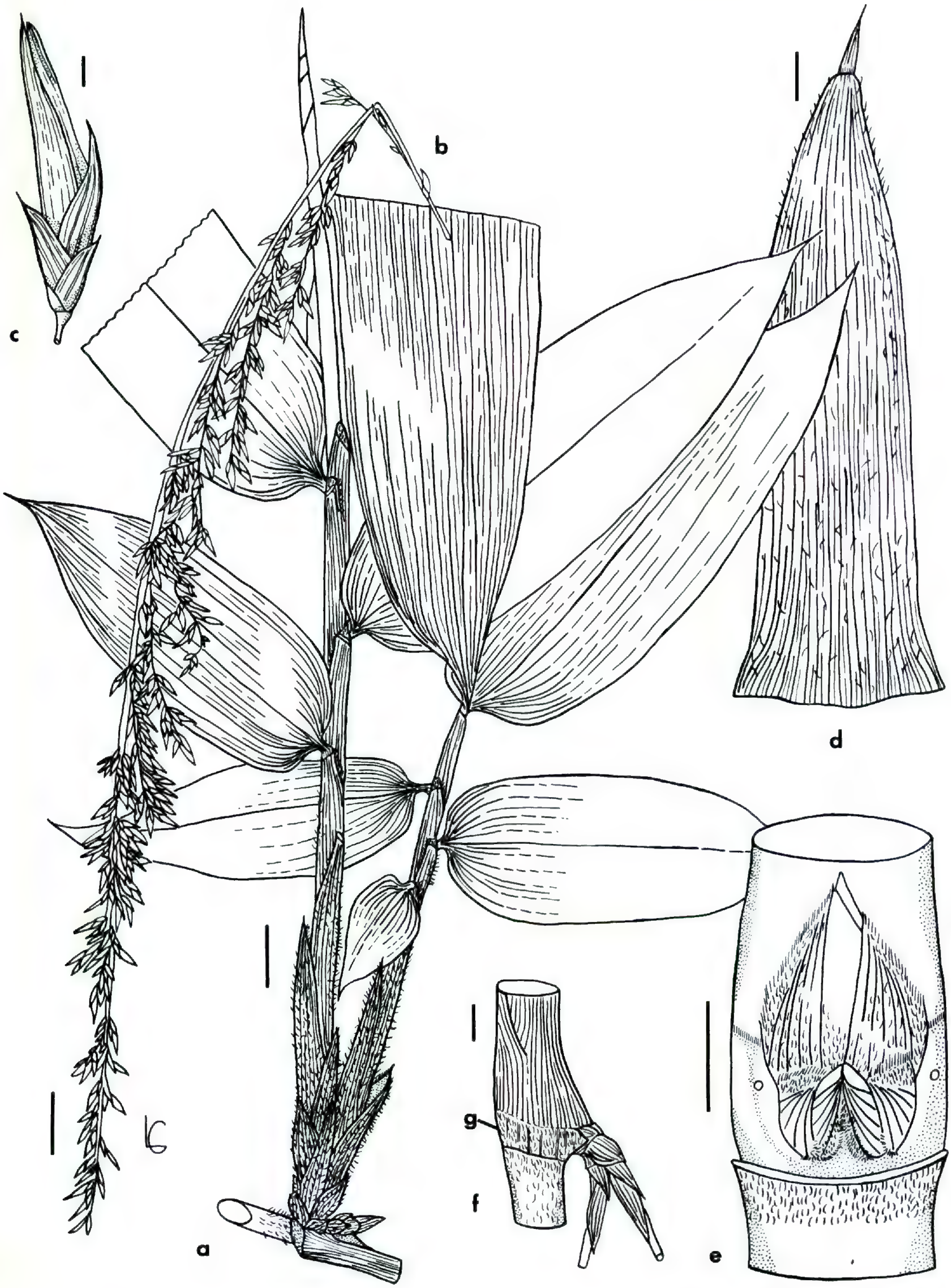

FIGURE 3. *Chusquea latifolia*.—A. Leafy branch complement, scale = 2 cm (based on *Killip & García 33904*).—B. Inflorescence, scale = 2 cm.—C. Spikelet, scale = 1 mm (B, C based on *García-Barriga 12259*).—D. Culm leaf, scale = 2 cm.—E. Bud complement, scale = 1 cm (D, E based on *Calderón 2997*).—F. Node with branches emerging infravaginally (base of sheath with fused margins), scale = 1 cm (based on *McClure 21748*).—G. girdle.

that rebranch extensively from their lower nodes. *Foliage leaves* 5–9 per complement; sheaths carinate, usually pubescent, especially along the keel, occasionally glabrous, the margins usually glabrous or occasionally sparsely ciliate; blades lanceolate to broadly lanceolate, 13.3–32.1 cm long, 3–8.5 cm wide, L : W = 3.5 : 6, the adaxial surface glabrous, not tessellate, the abaxial surface glabrous, weakly tessellate, the apex acuminate, the margins cartilaginous, serrulate, the base rounded to rounded-truncate; pseudopetiole distinct, 3–9 mm long; outer ligule a conspicuous, stiff rim 0.5–2 mm long; inner ligule usually conspicuous, rounded to truncate, (1–)2–15 mm long, usually abaxially pubescent at least on the lower half, chartaceous. *Inflorescence* a narrow panicle 20.5–42.5 cm long; rachis glabrous, one side flat and slightly ridged, the other rounded; branches appressed, secund, arising only from the flat, slightly ridged side of the rachis, angular, 3–9 cm long at the base of the panicle, becoming progressively shorter toward the apex with the spikelets eventually arising directly from the rachis, glabrous; pedicels short. *Spikelets* ovate-lanceolate, 8.2–12 mm long, slightly falcate. *Glumes* 2; glume I triangular, 0.5–1.3 mm long, apically rounded, glabrous, lacking nerves; glume II ovate-lanceolate, 2.4–2.5 mm long, apiculate, abaxially glabrous, adaxially sparsely pubescent near the apex, 3- or 5-nerved. *Sterile lemmas* 2; sterile lemma I ovate-lanceolate, 3.2–4.2 mm long, apiculate, abaxially glabrous, adaxially pubescent below the apex, 7- or 9-nerved; sterile lemma II ovate-lanceolate, 4.4–6.5 mm long, apiculate, abaxially glabrous, adaxially pubescent just below the apex, 7-nerved. *Fertile lemma* ovate-lanceolate, shiny, 8–10.6 mm long, apiculate, glabrous, 9- or 11-nerved. *Palea* ovate-lanceolate, 2-keeled, sulcate, shiny, 8.3–9.6 mm long, glabrous, 6- or 8-nerved, the apex acute but not apiculate. *Lodicules* 3; anterior pair 2.5–2.7 mm long, the upper margins ciliate; posterior lodicule 1.6 mm long, narrower than the anterior, ciliate on the upper margin. *Stamens* 3; anthers linear, 4.5–5.2 mm long. *Ovary* glabrous, with 2 styles bearing plumose stigmas. *Fruit* unknown.

Representative specimens examined. COLOMBIA. ANTIOQUIA: en selvas densas y húmedas en las montañas al oeste de Sonsón, *Johnson & Barkley 18C822* (COL). RISARALDA-QUINDIO: Río Barbas, *McClure 21748* (ISC, US). VALLE: old Cali–Buenaventura road, 17 km NW from Cali, Villa Monica–El Rancho de Yo, *Calderón 2997* (COL, ISC, US); Cordillera Occidental, vertiente oriental, hoya del río Cali, vertiente derecha confluencia del río Pichindecito con el Pichindé, 7 Nov. 1944 (fl), *Cuatrecasas 18767* (US); Cordillera Occidental, vertiente oriental, hoya del río Cali, río Pichindé, en Los Carpatos, *Cuatrecasas 21629* (US); San Antonio, W of Cali, near summit of Cordillera Occidental, *Killip & García 33904* (US); along Cali–Buenaventura Hwy. on E slope of Cordillera Occidental, *McClure 21234* (ISC, US).

This species is characterized by its large, wide leaves, rebranching subsidiary branches, scabrous sheath with a relatively small blade, and somewhat falcate spikelets with apiculate (but not distinctly awned) lemmas. Known only from Colombia, *Chusquea latifolia* generally inhabits cloud forests and ranges from 1,600 to 2,700 m elevation, although it may be found as high as 2,950 m in subparamo vegetation. The vine forms an extensive network, which clambers over trees and other vegetation. Frequently portions of the culm will run for several meters over the ground, eventually turning downward and entering the soil to re-emerge as another culm some distance away.

The bud complement of *C. latifolia* is unusual, consisting of one triangular central bud subtended by two (sometimes three) smaller, subequal subsidiary buds that begin to proliferate early (Fig. 3E). The central bud frequently does not develop, but the subsidiary buds develop and rebranch vigorously, often producing mature branch complements of up to 12 branches. Nodes of the main culm contain one root primordium on each side of the central bud (or branch). The nodal region of the culm is well marked, this band of tissue usually appearing slightly darker in color and being rugose in texture. The rhizomatous segments of the culm may be distinguished by their lack of such differentiation in the nodal region.

3. **Chusquea serpens** Clark, sp. nov. TYPE: Costa Rica. Alajuela: edge of Valley of Río Cariblanco, Cariblanco, 830 m, 26 Aug. 1968 (fl), *Pohl & Davidse 11023* (holotype, ISC; isotype, US). Figure 4.

Culmi scandentes, usque ad 1 cm diam., usque ad 20 m longi. Folia culmorum non persistentia, usque ad media internodia, 10–20.1 cm longa: vaginae rectangulares, latus factus basi, 6.7–11.3 cm longae, 2.5–4 cm lati basi, glabrae vel verrucosae trichomatibus rigidis, sparsis usque ad densis; laminae plus minusve cordatae, apicibus setosis, 3–8.4 cm longae, non longior quam vagina, glabrae; cingulum plus minusve prominens, usque ad 5 mm longum, confertim pubescens. Nodi ad culmum medium gemma centralis singularis triangularis subtenta a 2 gemmis parvioribus subaequantibus. Ramificatio infravaginalis. Folia 3–7 in

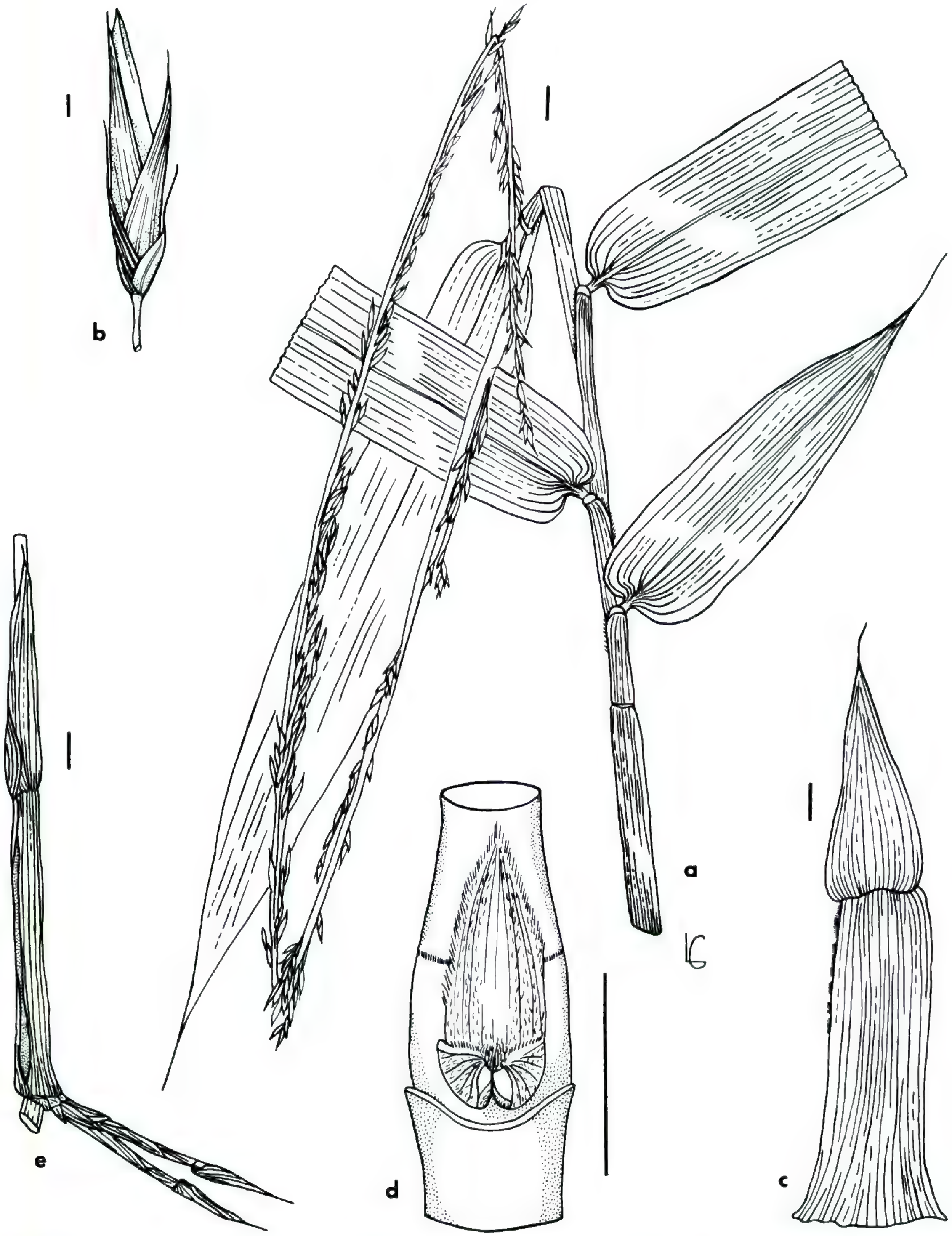

FIGURE 4. *Chusquea serpens*.—A. Flowering branch, scale = 1 cm (based on *Pohl & Davidse 11023*).—B. Spikelet, scale = 1 mm (based on *Pohl & Davidse 11176*).—C. Culm leaf, scale = 1 cm (based on *Young 101*).—D. Bud complement, scale = 1 cm.—E. Node with branches emerging infravaginally, scale = 1 cm (D, E based on *Clark 283*).

complemento: vaginae plerumque glabrae; laminae lineares-lanceolatae vel lanceolatae apicibus setosis, basibus rotundatis-truncatis, 11.7–35.8 cm longae, 1.8–5.1 cm latae, glabrae superne, plerumque glabrae inferne, pilosae solum ad apicem vel omnino pilosae, non tessellatae vel inferme ita; ligula interna truncata, 1–2(–2.5) mm longa. Inflorescentia angusta, paniculata, 33–55(–60) cm longa; rhachis complanata, glabra; rami appressi, secundi, angulati, glabri vel pilosi. Spiculae ovatae-lanceolatae, 11.3–14.6 mm longae. Glumae 2: glume I triangulata vel lanceolata, apice rotundatis, 1.2–2.5 mm longa, 1-nervis; gluma II ovata-triangularis, longa-aristata, 3.5–7 mm longa, 1- vel 3-nervis. Lemmata sterilia 2: lemma sterile I ovatum-lanceolatum, aristatum, 5.4–8.6 mm longum, (5–)7(–9)-nerve; lemma sterile II ovatum-lanceolatum, carinatum, brevi-aristatum, 7.7–9.9 mm longum, (5–)7–9- vel 11-nerve. Lemma fertile ovatum-lanceolatum, naviculare, aristatum, 10.6–13.2 mm longum, 7–18-nerve obscure. Palea ovata-lanceolata, apice bicarinata, sulcata, apiculata, 10.1–11.5 mm longa, 2–4(–6–8)-nervis.

Rhizomes leptomorph. *Culms* viny, scandent, to 1 cm diam., to 20 m long, often trailing for part of the length. *Internodes* terete but often shallowly sulcate above the primary bud, solid, to 39 cm long, retrorsely scabrous for most of their length, glabrous just above the node, green to green-mottled with purple. *Culm leaves* not persistent, extending about halfway up the internode, 10–20.1 cm long, chartaceous; sheaths more or less rectangular but flaring slightly at the base, loosely wrapped around the culm, 6.7–11.3 cm long, 2.5–4 cm wide at the base, usually about 1.5 times as long as the blade, occasionally equalling the blade, or to twice as long as blade, glabrous to verrucose with sometimes numerous rigid hairs,the overlapping margin ciliate; blades usually deciduous before sheaths separate from the culm, moderately to distinctly cordate, 3–8.4 cm long, not longer than the sheath, glabrous, the apex setose, the margins smooth to ciliate in some specimens; girdle more or less prominent, to 5 mm wide, densely pubescent, forming a flap through which the branches emerge, disintegrating before the rest of the culm leaf; inner ligule a short, ciliolate rim; outer ligule lacking. *Nodes* only slightly swollen, at mid-culm with one triangular central bud subtended by two smaller subequal buds. *Branching* infravaginal, central bud often developing into a robust branch more or less equal in size to the main culm, this branch rebranching extensively, forming a long clambering network; subsidiary buds 2, developing into leafy branches 15–35 cm long that rarely rebranch. *Foliage leaves* 3–7 per complement; sheaths carinate, usually glabrous, occasionally scabrous or pubescent near the margins and/or apex, the overlapping margin ciliate; blades linear-lanceolate to lanceolate, 11.7–35.8 cm long, 1.8–5.1 cm wide, L : W = 5 : 9, the adaxial surface glabrous, not tessellate, the abaxial surface mostly glabrous and pilose only near the apex to entirely pilose, not tessellate to weakly so, the apex tapering into a long bristle-like tip, the margins cartilaginous, serrulate, the base rounded-truncate; pseudopetiole distinct, 3–12 mm long; outer ligule a conspicuous, stiff rim 0.5–1.5(–2.5) mm long; inner ligule truncate, 1–2(–2.5) mm long, chartaceous. *Inflorescence* a narrow panicle 33–55(–60) cm long, terminating either a primary or subsidiary branch; rachis glabrous, one side flat and slightly ridged, the other rounded; branches appressed, secund, arising only from the flat, slightly ridged side of the rachis, angular, 5–9 cm long at the base of the panicle, becoming progressively shorter toward the apex with the spikelets eventually arising directly from the rachis, glabrous or pilose; pedicels short. *Spikelets* ovate-lanceolate, 11.3–14.6 mm long. *Glumes* 2; glume I somewhat variable, triangular to lanceolate, 1.2–2.5 mm long, apically broadly acute, glabrous, 1-nerved; glume II ovate-triangular, 3.5–7 mm long, long-awned, glabrous to slightly pubescent adaxially just below the apex, 1- or 3-nerved. *Sterile lemmas* 2; sterile lemma I ovate-lanceolate, 5.4–8.6 mm long, awned, glabrous to densely pubescent adaxially, (5–)7(–9)-nerved; sterile lemma II ovate-lanceolate, keeled, 7.7–9.9 mm long, awned, glabrous to densely pubescent adaxially for the upper one-half to two-thirds of its length, (5–)7–9- or 11-nerved. *Fertile lemma* ovate-lanceolate, boat-shaped, shiny, 10.6–13.2 mm long, short-awned, glabrous to densely pubescent adaxially for the upper one-half of its length, usually obscurely 7–18-nerved. *Palea* ovate-lanceolate, 2-keeled, sulcate, shiny, 10.1–11.5 mm long, apiculate, marginally ciliate toward apex, glabrous, 2–4(–6–8)-nerved. *Lodicules* 3; anterior pair 2–2.5 mm long, the upper margins ciliate; posterior lodicule 2.5–3 mm long, narrower than the anterior, ciliate on the upper margins. *Stamens* 3; anthers linear, 5.5–7.5 mm long. *Ovary* glabrous, with 2 styles bearing plumose stigmas. *Fruit* unknown.

Representative specimens examined. COLOMBIA. CAQUETÁ: Cordillera Oriental, vertiente oriental, Sucre, 4 Apr. 1940 (fl), *Cuatrecasas 9068* (COL, F, US). HUILA: Río Ambicá, near Quebrada San Pedro, 18 km SE of Colombia, 24 Dec. 1942 (fl), *Fosberg & Holdridge 19568* (US). META: Las Lagartijas, plateau between Río

Papamene and Río Duda, Colombia–Uribe trail, 8–9 km SW of Uribe, 22 Dec. 1942 (fl), *Fosberg 19504* (US). COSTA RICA. ALAJUELA: Cariblanco, across bridge N of village, along Río Cariblanco, *Clark et al. 283* (ISC); Cataratas de San Ramón, *Ocampo 1326* (CR, ISC, US); edge of valley of Río Cariblanco, Cariblanco, 29 Sept. 1968 (fl), *Pohl & Davidse 11176* (ISC). SAN JOSÉ: Tinamastes, 13 km SW of San Isidro de El General on road to Dominical, *Pohl 14187* (ISC). ECUADOR. NAPO: 5 km E of the town of Reventador on the road to Lumbaqui, *Young 101* (US). PANAMA. BOCAS DEL TORO: between Buenavista coffee finca and Cerro Pilón, on Chiriquí trail, cloud forest, 17 Apr. 1968 (fl), *Kirkbride & Duke 692* (MO). CHIRIQUÍ: vicinity of Gualaca ca. 8.5 mi. from Planes de Hornito, La Fortuna on road to damsite, *Antonio 5089* (MO, US). PANAMA/COLOMBIA. DARIÉN/CHOCÓ: Alto de Nique, southernmost peak of Cerro Pirre massif, *Gentry et al. 28692* (US). VENEZUELA. LARA: Dtto. Morán, road between Guarico and Villa Nueva, going toward Villa Nueva a little past the hill at 1,640 m, Oct. 1978 (fl), *Burandt VO457* (MO); Parque Nacional Yacambú, ca. 6–10 km from main entrance, at a picnic area, *Clark et al. 231* (ISC); Guarico, San Isidro, 22 Sept. 1942 (fl), *Tamayo 2476* (VEN). MÉRIDA: rich damp forest along NW- and W-facing slopes of Quebrada de Montaña, in La Montaña de Los Torritos, tributary to Río Canaguá, above Finca La Montaña, 8 km SW of Canaguá, *Steyermark 56392* (US).

Chusquea serpens is characterized by its viny, stoloniferous habit, branch complement with only two subsidiary branches, cordate culm leaf blade almost equal to the sheath in length, secund inflorescence, and awned spikelets. *Chusquea serpens* and *C. latifolia* are similar in many respects, particularly in their clambering habit, bud complement of one triangular central bud subtended by two subsidiary buds, and large, secund inflorescences (not so marked in *C. latifolia*). Both species clearly fall within *Chusquea* because of their solid culms, multiple independent buds, and typical one-flowered spikelets but may form a natural group within the genus based on the unusual nature of the bud complement. *Chusquea serpens* can be distinguished from *C. latifolia* by its generally less robust appearance, relatively larger, cordate culm leaf blade, and awned spikelets. *Chusquea serpens* has appeared previously in the literature as the "Cariblanco population" of *Chusquea* and *Chusquea* "*cariblanco*" (Pohl, 1980, 1983).

Chusquea lanceolata Hitchcock from Guatemala and Mexico, closely related to *C. serpens,* differs in its relatively smaller culm leaf blades, more open inflorescences, and spikelets with apiculate, not awned, lemmas. The two species are very similar with respect to their clambering habit, branch complement, and large leaves. *Chusquea lanceolata* tends to occur at somewhat higher elevations than *C. serpens,* although still in the montane forest zone.

Chusquea serpens is the only species of *Chusquea* known to occur in both Central and South America, extending from Costa Rica to Venezuela and along the Andes to Ecuador. It is found in cloud forests throughout its distribution, ranging in elevation from 800 to 2,100 m. Typically the plant forms large, tangled networks that festoon the surrounding vegetation. In contrast to *C. latifolia,* the central branches in *C. serpens* rebranch to produce the long, trailing and hanging culms.

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NOTES

PHARUS PARVIFOLIUS SUBSP. *ELONGATUS* (POACEAE), A NEW SUBSPECIES FROM TROPICAL AMERICA

While working on a revision of the Phareae (Poaceae: Bambusoideae), it became evident that the widespread neotropical species *Pharus parvifolius* Nash consists of two entities that merit subspecific recognition. The present note is necessary to validate the name of the new taxon, so that it will be available for use in my Flora Mesoamerica treatment. A more detailed study of this species will be presented in a forthcoming revision of *Pharus*.

Pharus parvifolius was described from Haiti (Nash, 1908). It is differentiated from other species in the genus by its colonial habit (old culms become decumbent and root at the nodes), strongly two-ranked foliage, lower (morphologically adaxial, as in all species in the Phareae) leaf blade surfaces with longitudinal sclerenchymatous bands between the small lateral veins, and linear-oblong pistillate spikelets with purple glumes.

Subspecies *parvifolius* is characterized by the following features: erect stems 25–50 cm long; leaf blades lanceolate, 6.5–15 cm long, 1–2.5 cm wide, asymmetrical, the apex attenuate, the lateral veins diverging from the midrib by 7–11°; panicle 8–15 cm long, the (naked) axis terminating the inflorescence 2–5 cm long; and pistillate spikelets 8–14 mm long. It is frequent in Cuba, Hispaniola, eastern Venezuela, and Surinam, with scattered stations in Central America, the smaller West Indian islands, French Guiana, Ecuador, and Brazil.

A more robust series of populations, widely distributed in the Neotropics but with a concentration of sites in Central America, is described.

Pharus parvifolius Nash subsp. **elongatus** Judziewicz, subsp. nov. TYPE: Costa Rica. Cartago: Los Espaveles Nature Trail into forested canyon of the Río Reventazón, Centro Agronómico Tropical de Investigación y Ensenanza (CATIE), 3 km E of Turrialba, 9°54′ N, 83°39′W, 550–600 m, 9 May 1983, in young fruit, *Liesner, Judziewicz & Pérez 15281* (holotype, CR; isotypes, BAF, BM, CEPEC, COL, CR, CTES, DUKE, F, IBUG, INPA, ISC, LE, LPB, MEXU, MO, MVFA, NY, P, PMA, RB, SP, US, VEN, WIS, XAL).

Differt a *P. parvifolius* subsp. *parvifolius* statura altiore (60–125 cm), laminae lineare-lanceolatae longiore (18–32 cm) latioreque (2–3.5 cm), nervi sub angulo 4–8°, inflorescentiae longiore (20–35 cm), axis terminalae longiore (3.5–9 cm), et spiculae feminae longiore (10–16 mm).

Similar to subspecies *parvifolius*, but larger: culms stout, 3–6 mm diam.; erect culms 60–125 cm long; leaf blades linear to linear-lanceolate, 18–32 cm long, 2–3.5 cm wide, tapering to both base and apex, the lateral veins diverging from the midrib by 4–8°, panicle 20–35 cm long, the naked, terminal portion of the axis 3.5–7(–9) cm long; pistillate spikelets slightly larger than in the typical variety; glumes 5.5–8 mm long, lemma 10–16(–17) mm long.

Representative specimens examined (only one given per country). MEXICO. VERACRUZ: Estación Biológica Los Tuxtlas, *Calzada 1186* (ENCB, F, MEXU). BELIZE. TOLEDO: 2–3 mi. down trail beginning 1 mi. N of Columbia Forest Station, *Vanderveen 631* (MO). HONDURAS. ATLANTIDA: Río Esperanza, near Elver's, *Wilson 548* (US). NICARAGUA. JINOTEGA: Cerro El Congo, Comarca Kilambe, 13°35′N, 85°37′W, 955 m, *Sandino 112* (MO). COSTA RICA. GUANACASTE: W side of Volcán Rincón de la Vieja, 1,150 m, *Pohl 12667* (F, ISC, MO, US). PANAMA. CANAL AREA: Barro Colorado Island, *Foster 1766* (DUKE, F, GH, MICH, PMA). JAMAICA. PORTLAND: Gorge of Stony River below junction of Macungo River, 1,200 ft., *Proctor 31245* (ENCB, LL). HAITI. NORD-OUEST: Massif du Nord, Port-de-Paix, 150 m, *Ekman H-3825* (S, US). SURINAM. Between Kabalebo and Coppename Rivers, 20 km downstream from the Kabalebo airstrip, Bakhuis, *Florschütz & Maas 2523* (U). ECUADOR. MANABÍ: El Rosario, *Eggers 15188* (F, P, fragm. US ex K). PERU. LORETO: Puerto Arturo, *Williams 5285* (F, GH, LE, US). BRAZIL. BAHIA: Rio Gongogi, *Curran 110* (US). BOLIVIA. LA PAZ: Covendo, 2,000 ft., *White 1043* (US).

Both subspecies grow in the same habitat, moist to wet forests from near sea level to 1,000 m or more. The tendency toward geographical separation in these two entities, and their nearly absolute vegetative distinctness from each other (there are a few intermediate populations in northern Central America and Peru) suggest the rank of subspecies rather than variety. I do not believe that specific recognition is warranted. In addition to the intermediate specimens just mentioned, there is an apparent lack of temporal separation in flowering time between the two

subspecies, both blooming in the Northern Hemisphere dry season (about January to May). Also, although vegetatively most specimens can be assigned without much difficulty to one taxon or the other, there is a much greater degree of overlap in reproductive characteristics, especially in the pistillate spikelet.

Pohl and Davidse (1971) reported a chromosome number of $2n = 24$ (i.e., diploid, as in most other species in the genus) for the (now type) population of subsp. *elongatus* at Turrialba, Costa Rica. There are no chromosome counts of subsp. *parvifolius*.

Assistance was received from the E. K. and O. N. Allen and J. J. Davis Funds of the University of Wisconsin, Wisconsin Natural History Council, Museo Nacional de Costa Rica, and Missouri Botanical Garden. Thanks are due to H. H. Iltis, G. Davidse, R. L. Liesner, and T. H. Cochrane.

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CAMPYLOCENTRUM TENELLUM (ORCHIDACEAE), A NEW SPECIES FROM PANAMA

Campylocentrum Bentham is a genus of approximately 45 species of small, epiphytic, neotropical orchids. In a revision of the Costa Rican species (Todzia, 1980), a new taxon from Panama came to my attention. After careful examination of the South American taxa, I feel confident in proposing this new species.

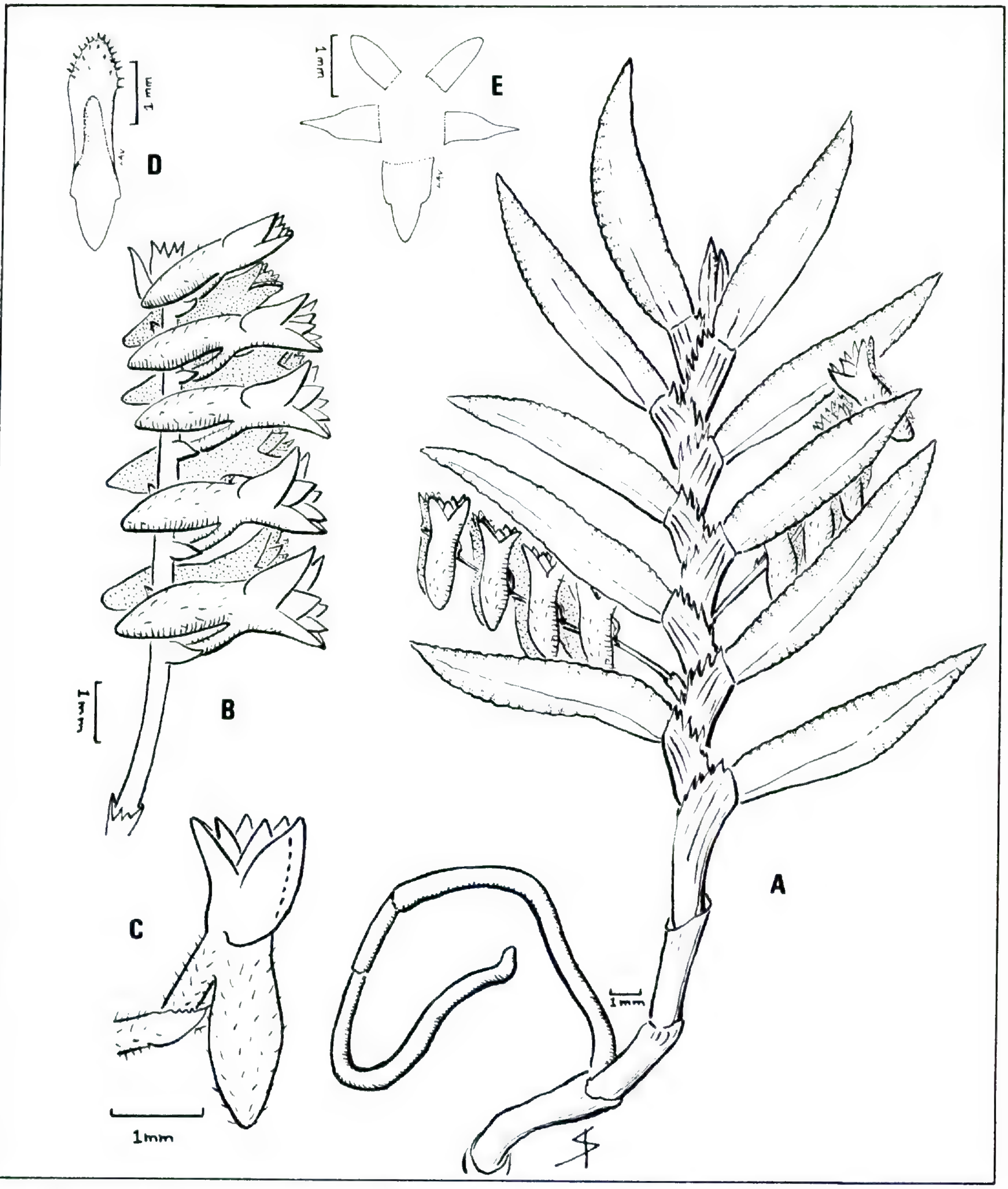

FIGURE 1. *Campylocentrum tenellum.*—A. Whole plant.—B. Raceme.—C. Flower.—D. Lip and spur.—E. Sepals, petals, and lip.

Campylocentrum tenellum Todzia, sp. nov. TYPE: Panama. Panamá: La Eneida, region of Cerro Jefe, 26 Oct. 1969, *Dressler 3758* (holotype, CR). Figure 1.

Planta parvula, epiphytica, 1–5.5 cm alta; folia lineario-lanceolata, 0.8–1 cm longa, 1–2 mm lata, vaginae tubulares, lacerae; inflorescentia 7–10 mm longa; flor albus, sepala ovata, petala lanceolata, labellum trilobatum, calcar rectum acutum hispidulum.

Small, epiphytic plant with pendant or ascending stems, 1–5.5 cm tall. Roots basal or alternating with the lower 1 or 2 leaves, fibrous, flexuous, glabrous, to 15 cm long. Stem simple, terete, slightly fractiflex, 1–2 mm wide, invested by leaf sheaths. Leaves small, thin, distichous, linear-lanceolate, margin smooth to lightly denticulate and crenulate, apex retuse, mucronulate to caudate, articulated to the persistent sheathing bases, 0.8–1 cm long, 1–2 mm broad; leaf sheath tubular, compressed, lacerate on the apical margin. Inflorescences produced singly opposite the leaves, not exceeding the leaves, ascendant to spreading, 7–10-flowered; rachis 7–10 mm long, minutely puberulent; floral bracts concave, triangular, acuminate, 1 mm long, ciliate along the margin. Flowers small, distichous, white to cream-colored; sepals ovate, acute, 1 mm long, 1-nerved, outer surface lightly hispidulous; petals linear, acute, 1.25 mm long, longer than the sepals, 1-nerved; lip ovate, 1.5 mm long, slightly 3-lobed at the base, lateral lobes obtuse, abbreviated, mid-lobe ovate, acute; spur straight, cylindric, acute, 1.5–2 mm long, outer surface lightly hispidulous; column short, 0.5 mm long; ovary 0.75–1 mm long, hispidulous with short, stiff hairs 0.1 mm long. Capsule not seen.

Additional collection. PANAMA. PANAMÁ: El Llano–Carti Hwy., 15–20 km N of El Llano, 30 Sept. 1973, *Dressler s.n.* (TEX).

Campylocentrum tenellum is most similar to *C. parvulum* Schltr. of Costa Rica, from which it is differentiated by its lacerate leaf sheaths, shorter inflorescences, and flowers with a longer spur. It is easily distinguished from all other leafy Panamanian *Campylocentrum* species by its straight, acute spur, thin, lanceolate leaves, lacerate leaf sheaths, and the small size of the plant. *Campylocentrum tenellum* belongs to section *Campylocentrum* as does *C. parvulum*.

I thank R. L. Dressler for making these specimens available to me, S. Thurston and L. Vorobik for graciously providing the drawing, and B. Simpson and M. C. Johnston for helpfully critiquing the manuscript.

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SAURAUIA MOLINAE, A NEW SPECIES OF ACTINIDIACEAE FROM CENTRAL AMERICA

In the course of preparing the taxonomic treatment of *Saurauia* (Actinidiaceae) for Flora Mesoamericana, I was not able to place a group of specimens recently collected from Honduras in the classification scheme of Hunter (1966) or Soejarto (1980). Nor do these specimens fit the recently described species of this genus from Mexico (Keller & Breedlove, 1981). Further study showed that these specimens belong to a new taxon described below.

Saurauia molinae Soejarto, sp. nov. TYPE: Honduras. Departmento de Comayagua: 3 km S of Siguatepeque, 1,300 m, thickets along creeks in pine forest; weak tree, flowers white, 9 Jan. 1969, *Molina 23296* (holotype, MO!; isotype, F!). Figure 1.

Saurauia molinae Soejarto; inter species seriei *Gynotrichae* foliis valde coriaceis indumento sepalorum expositorum in alabastro et inflorescentiarum omnino gossypino differt.

Trees, to 12 m tall. *Branchlets* terete, distinctly hollowed, with leaf scars prominent, sparingly to densely appressed pubescent, pubescence denser along juvenile parts and shoots, trichomes plumulose-setose to plumulose-sericeous, yellow to rusty brown. *Leaves* simple, penninerved, spirally arranged, clustered below tips of branchlets; blades obovate to elliptic-obovate, 10–25 cm long, 5–13 cm wide, coriaceous, in dry state dark to gray-brown adaxially, olive brown abaxially, much darker adaxially, rounded-acute to very shortly acuminate to rarely obtuse at apex, cuneate to broadly acute to obtuse to rounded, but less frequently oblique at base, subentire to finely setaceo-serrulate along margins, teeth or setae less than 1 mm long, 2–8 mm apart, secondary veins 14–25 pairs, forming a wide-angled V (becoming more acute toward apex) with straight to somewhat curving arms that lightly curve and usually dichotomize shortly before reaching margins and may or may not form a lightly anastomosing network, tertiary veins elevated beneath, more prominent than lesser reticulation; upper surface usually smooth and sometimes opaque or subglossy, scattered pubescent, trichomes limited primarily to major veins, yellow to white, hirsute to sericeous, appressed to the epidermal surface, tufted to barbate at their base; abaxial surface somewhat smooth, unevenly pubescent, denser along major veins, glabrous to glabrescent on other parts and between veins, trichomes along veins appressed to epidermal surface, plumulose-hirsute to plumulose-sericeous, mixed with and obscured by cottony or arachnoid indument in juvenile leaves, minor reticulation distinctly discernible; petiole subterete, lightly canaliculate adaxially, 2–4.5 cm long, 2–3 mm diam., abundantly to densely pubescent, trichomes to 4 mm long, plumulose-sericeous and mixed with arachnoid indument, the latter more distinct in juvenile leaves. *Inflorescence* a thyrse, inserted at 30° angle to perpendicularly to branchlet, straight, becoming somewhat pendulous in fruit, moderately branched, 15–90-flowered, 7–18 cm long, 4–9 cm wide, abundantly to densely pubescent especially on terminal parts, pubescence yellow-brown, cottony, individual trichomes plumulose-hirsute mixed with and obscured by the cottony indument, peduncle 3.5–9 cm long, bracts linear to subulate, to 5 mm long, densely cottony pubescent. *Flowers* actinomorphic, perfect, of two types, one short-styled belonging to functionally staminate plants, the other long-styled belonging to functionally pistillate plants, 13–18 mm broad when open, buds subglobose, to 5 mm across, pedicels 2–7 mm long, to 10 mm in fruiting stage, bracteoles linear to subulate, to 4 mm long, densely cottony pubescent; sepals 5, reflexed at apex early in bud, remaining so in fruit, aestivation quincuncial, outer two ovate to elliptic to oblong-elliptic to orbicular-ovate, acute at apex, imbricated one ovate-oblong to suborbicular, rounded at apex, inner two ovate-oblong to ovate-orbicular to suborbicular, rounded at apex, all 7–13 mm long, 6–13 mm wide, the outer two the smallest, all densely cottony pubescent on exposed parts in bud, glabrous on imbricated parts and inner surface, outer two entire to obscurely ciliate, inner three distinctly ciliate; petals 5, white, connate basally and falling off as a unit with stamens after anthesis, oblong to oblong-obovate to oblong-elliptic, 6–10 mm long, 3–5 mm wide, rounded at apex, rarely emarginate or incised; stamens 19–21, filament 2 mm long, pubescent at base, trichomes filiform, anther linear-oblong, 2 mm long, extrorse; ovary globose, 5-loculed, 5-sulculate, densely pubescent, tri-

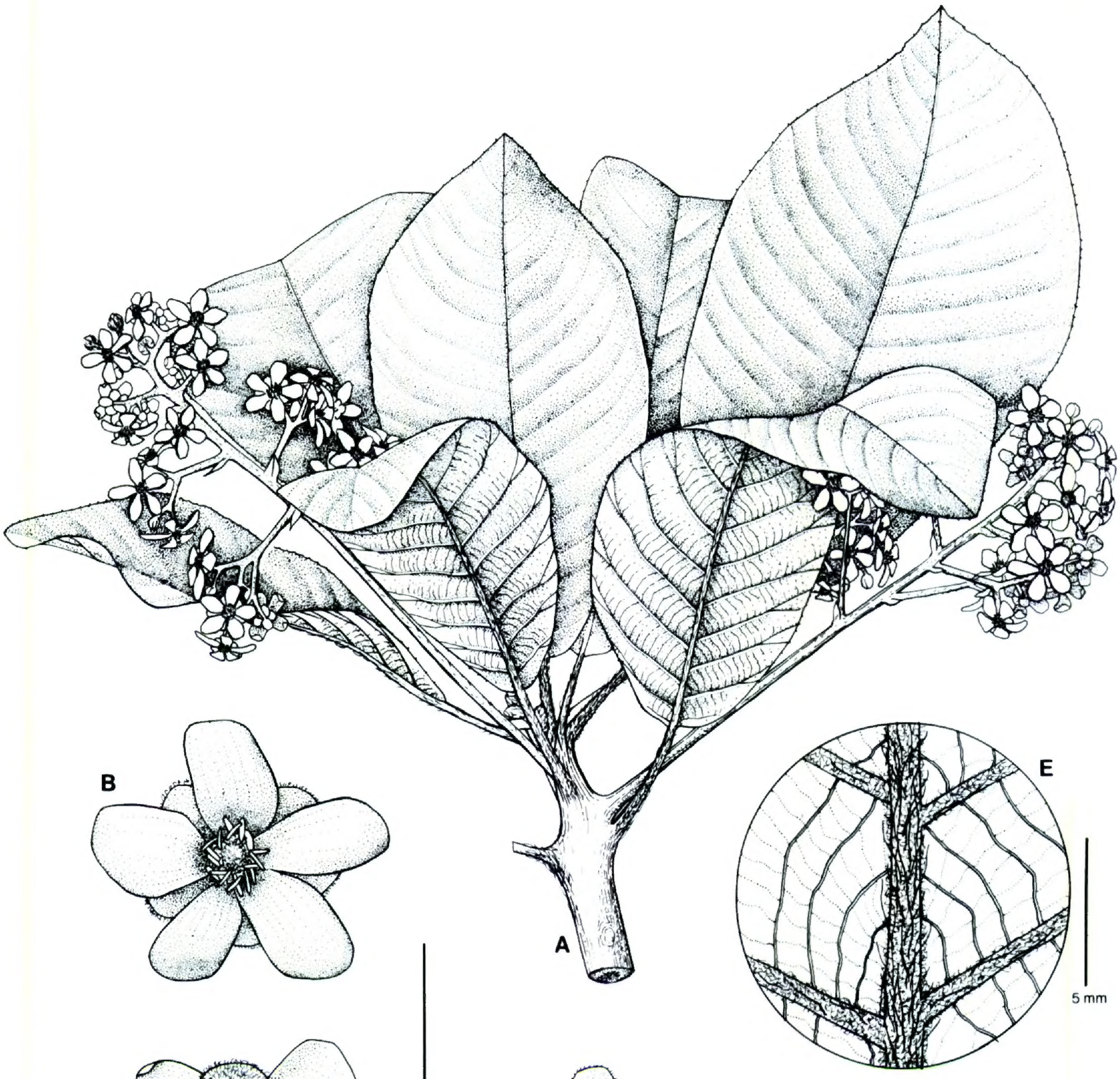

FIGURE 1. *Saurauia molinae* Soejarto.—A. Flowering branch from a functionally staminate plant.—B. A functionally staminate flower, top view; note the obsolete-styled, densely pubescent ovary surrounded by stamens.—C. A functionally staminate flower, bottom view, showing the pattern of pubescence on the outer surface of the sepals.—D. A fruit from a functionally pistillate flower.—E. Enlarged portion of the abaxial leaf surface to show details of venation and pubescence along the major veins. A–C, E are based on *Molina & Molina 25585* and *Molina 23296* (holotype); D is based on *Hazlett 1471*.

chomes yellow-brown, styles obsolete in functionally staminate plants, to 4.5 mm long in functionally pistillate plants, stigmas simple to subcapitate. *Berries* globose, 5-loculed, 5-sulcate, sparingly to abundantly pubescent (epidermal surface of ovary usually visible), trichomes yellow-brown, of fimbriate-stellate type, with arms straight or wavy, hyaline and filiform, to 1 mm long and upwardly appressed, styles 5, persistent, to 5 mm long, sepals persistent.

Additional specimens examined. HONDURAS. DEPT. COMAYAGUA: 10 km W of Siguatepeque, between El Portillo and El Porvenir, 1,300 m, cut-over forest, weak tree, flowers white, 10 Mar. 1970, fr., *Molina & Molina 25455* (F); 10 km W of Siguatepeque, new highway to the N coast, 1,200 m, cut-over mixed forest, ravine, tree 5–12 m, common, flowers white, "Capuchin de Montaña," 18 Apr. 1971, fr., *Molina 25985* (F); S of Siguatepeque, tree beside stream that passes through Potrerillos, 21 Apr. 1974, fr., *Hazlett 1471* (MO). DEPT. INTIBUCA: Quebrada Lejarsia, between Kms 9 and 11 on road La Esperanza–Marcala, 1,600 m, open forest, weak tree, 8 m, common, 21 Mar. 1969, fr., *Molina & Molina 24300* (F); Cordillera Opalaca, Pela Nariz, 1,900 m, cut-over cloud forest, weak tree, 6 m tall, flowers white, 13 Mar. 1970, fl., *Molina & Molina 25585* (F). DEPT. LA PAZ: Cordillera Guajiquiro, between Las Marias and El Cerron, 1,700 m, cut-over mixed forest, tree 12 m, flowers white, 20 Mar. 1969, fr., *Molina & Molina 24232* (F).

This new taxon belongs to the series *Gynotrichae* (Hunter, 1966). Like all other members of this series (*S. veraguasensis* Seem., *S. squamifructa* Hunter, and *S. waldheimia* Busc.), it is characterized by the possession of pubescent ovary.

S. molinae Soejarto may be distinguished from the other Central American members of the series by the following key:

1a. Leaves with stellate trichomes throughout the abaxial surface.
  2a. Inflorescences usually more than 10-flowered ..... *S. veraguasensis*
  2b. Inflorescences usually less than 7-flowered ..... *S. squamifructa*
1b. Leaves without stellate trichomes on the abaxial surface or, if present, limited only to the axils of secondary veins.
  3a. Blades chartaceous, normally less than 15 cm long, axils of secondary veins villous-barbate abaxially, sepals with appressed-setulose or plumulose-setulose trichomes on the exposed surface in bud ..... *S. waldheimia*
  3b. Blades coriaceous, normally more than 15 cm long, axils of secondary veins not villous-barbate abaxially, sepals cottony pubescent on the exposed surface in bud ..... *S. molinae*

The new taxon is dedicated to Dr. Antonio Molina, the Honduran botanist, whose extensive explorations of the flora of Honduras resulted in the discovery of this species.

I would like to thank Ms. Marlene H. Werner, a senior scientific illustrator of the Field Museum of Natural History, who kindly prepared the illustration.

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ERRATA

The following corrections should be made in the paper titled "The order Myrtales: circumscription, variation, and relationships," by Rolf Dahlgren and Robert F. Thorne [71(3): 633–699. 1984 (1985)]. A and B should be switched in the legend to Figure 1. The legend to Figure 14 should be switched with the legend to Figure 16.

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